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CONTENTS

Larger cryptostome Bryozoa of the Ordovician and Silurian, Anticosti Island, Canada—Part I ..... *June Phillips Ross* 1057

Some Mississippian fenestrate Bryozoa from Central Utah ..... *Lloyd H. Burckle* 1077

An interesting Late Cretaceous calcareous alga from Guatemala ..... *J. Harlan Johnson* and *Kenji Konishi* 1099

The brachiopod genera *Ingelarella* and *Notospirifer* in the Permian of Queensland ..... *K. S. W. Campbell* 1106

Mississippian ammonoids from northwestern Canada ..... *D. H. A. Sellers* and *W. M. Furnish* 1124

Montecaris lehmanni, a new crustacean from the Rhenish Devonian and the problem of its systematic position ..... *Ulrich Jux* 1129

Calcisphaera from the Salem (Mississippian) limestone in southwestern Illinois ..... *James W. Baxter* 1153

Early Ludlow graptolites from the Ashland Area, Maine ..... *William B. N. Berry* 1158

Foraminiferal biofacies off the South China coast ..... *Harry O. Waller* 1164

A paleoecologic study of the Upper Denton Formation, Tarrant, Denton, and Cooke counties, Texas ..... *L. Ronald Laughbaum* 1183

Ptychoblastus, a new Mississippian blastoid from Missouri ..... *Robert O. Fay* 1198

Conodonts from the Glen Dean Formation of Kentucky and equivalent formations of Virginia and West Virginia ..... *Carl B. Rexroad* and *Charles E. Clarke* 1202

Pliocene fresh-water gastropods from San Mateo County, California ..*William Glen* 1207

New name for *Spirifer occidentalis* (Girty) and its geologic history ..*Walter Sadlick* 1210

PALEONTOLOGICAL NOTE

Mosasaur remains from the Upper Cretaceous of Western Australia ..... *Ernest Lundelius, Jr.* and *S. St. J. Warne* 1215

NOMENCLATURAL NOTE

Emendations to Upper Pennsylvanian arenaceous Foraminifera from Kansas ..*H. A. Ireland* 1217

INDEX 1219

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VOLUME 34 NOVEMBER, 1960 NUMBER 6

LARGER CRYPTOSTOME BRYOZOA OF THE ORDOVICIAN AND SILURIAN, ANTICOSTI ISLAND, CANADA—PART I

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ABSTRACT—The larger cryptostome Bryozoa from the late Ordovician and early and middle Silurian strata of Anticosti Island when studied by thin section techniques consist of nine species, two of which are new, *Ptilodictya denticulata* and *Pachydictya* n. sp. Seven of the species had previously been given a total of sixteen names. *Ptilodictya denticulata* is restricted to the English Head formation (upper Ordovician) and *Phaenopora superba* first appears in the Becscie formation (lower Silurian) and extends into the overlying Gun River formation (lower Silurian). The other cryptostome bryozoan species range from the late Ordovician into the early and middle Silurian strata except for two species of *Stictopora* which are found only in the upper Ordovician. Comparison of the bryozoan faunas and other Anticosti Island faunal elements with those in other areas from late Ordovician and early Silurian strata suggests the English Head, Vaureal, and Ellis Bay formations are equivalent in age to the Richmond group, Ohio, and it does not support the placement of these Anticosti beds into a "Gamachian Series" of post-Richmond but pre-Silurian age.

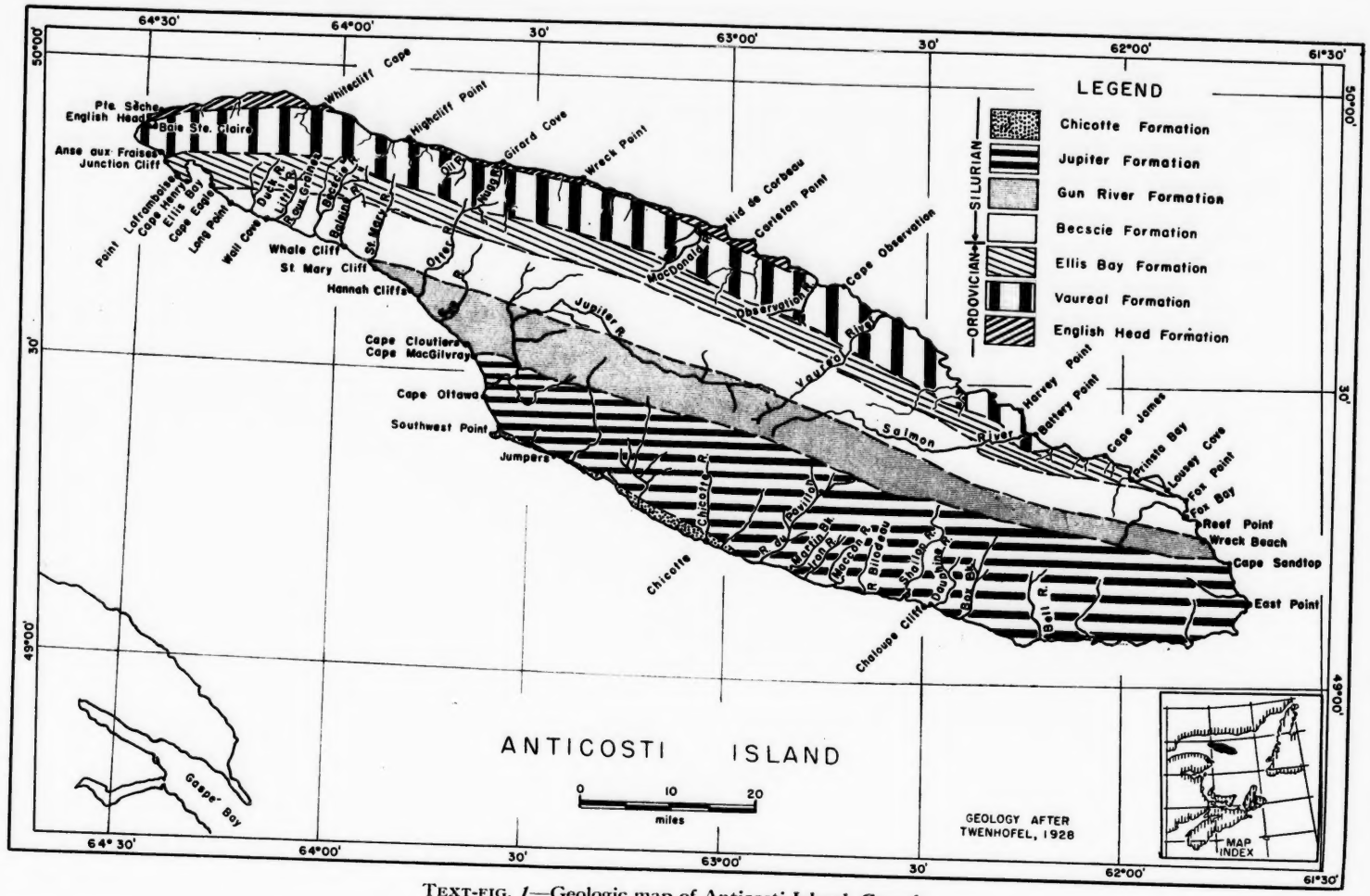
Based on skeletal microstructures observed in type material and additional material, the five species of *Ptilodictya* and one species of *Stictoporella*, *S. excellens*, described in this paper may be conveniently assigned to the informal taxonomic category of the escharoporid group.

INTRODUCTION

THE present study results from investigation of the larger part of W. H. Twenhofel's extensive fossil collection from various localities on Anticosti Island, Canada (Text-fig. 1), made in 1909 and 1919.

Examination of a number of species of larger cryptostome Bryozoa based on the original type material and additional material has resulted in many changes in the stratigraphic distribution of the species. The smaller cryptostome Bryozoa are not investigated in this study but they also require extensive revision. In view of these problems in the Bryozoa it seems that similar studies in other invertebrate groups might yield new data for the Ordovician and Silurian faunas of Anticosti Island.

Bryozoa are abundant in the 2,400 feet of calcarenite, calcilutite, calcirudite, and biohermal limestone strata of Ordovician and Silurian age on Anticosti Island. They are well represented in the faunas from the English Head, Vaureal, and Ellis Bay formations of late Ordovician (Richmond) age and the Becscie, Gun River, Jupiter, and Chicotte formations of early to middle



TEXT-FIG. *1*—Geologic map of Anticosti Island, Canada.

Silurian age. Cryptostomatous Bryozoa are abundantly distributed throughout these rocks (Table 1) and are sparse only in the Vaureal formation which has mainly a trepostome assemblage.

The Bryozoa which are described in the following pages have been fitted into the various formations as outlined by Twenhofel (1928) who contributed so extensively to the geology of Anticosti Island at the mouth of the St. Lawrence River. As Twenhofel's formations are a grouping of faunal zones, not necessarily representing distinct lithologic units, the placement of certain localities has been difficult. With further field investigation some of these faunal zones will probably be found to be facies equivalent.

Acknowledgments.—I am indebted to C. O. Dunbar, Yale University, who suggested the investigation; G. A. Cooper and R. S. Boardman, U. S. National Museum; H. Frebold, P. Harker, and T. Bolton, Geological Survey of Canada; and N. Newell, American Museum of Natural History, for the loan of material from various collections. I wish to thank Dr. Bolton for helpful information on the stratigraphy of Anticosti Island, Miss Helen Duncan, U. S. Geological Survey, for discussion of Ordovician faunas, and J. Berdan, U. S. Geological Survey, for discussion of Ordovician and Silurian Ostracoda. The sketches are the work of C. A. Ross, Yale University. The work was undertaken during the tenure of a Research Fellowship from Yale University.

Abbreviations of repositories.—AMNH—American Museum of Natural History; GSC—Geological Survey of Canada; USNM—U. S. National Museum; YPM—Yale University, Peabody Museum.

COMPOSITION AND AGE OF THE FAUNAS

Although 16 species of larger cryptostome Bryozoa were described from the Anticosti Island sequence in Twenhofel (1928) only seven species are now recognized. These species are *Ptilodictya canadensis* Billings, *P. denticulata* Ross, n. sp. *P. ensiformis* (Hall), *P. sulcata* Billings, *Phaenopora superba* (Billings), *Stictoporella excellens* (Billings), and a new species of *Pachydictya*. In addition, two species of *Stictopora*,

TABLE 1—DISTRIBUTION OF SPECIES

| SPECIES | ORDOVICIAN | | | | | | | | | | | | | | | | | | | | | | | | | | SILURIAN | | | | | | | | | | | | | | | | | | |

Stictopora sp. A and *Stictopora* sp. indet., have been found. The ranges of these bryozoan species are given in Table 1.

In the English Head formation, *Ptilodictya denticulata* Ross, n. sp., a distinctive species, occurs in siliceous calcarenite. It has close affinities with *P. magnifica* Miller from the Whitewater member, Richmond group. *P. sulcata*, *P. candensis* and *P. ensiformis*, and *Pachydictya* n. sp. are found in calcarenite having a finely comminuted calcite matrix.

In the Vaureal formation, *Ptilodictya sulcata* is the most abundant species and *Stictopora* sp. A first appears in fine calcarenite.

In the Ellis Bay formation, *Pachydictya* n. sp. occurs as large fragmented colonies in coarse calcarenite and is abundantly distributed at various horizons throughout the formation. *Ptilodictya ensiformis* occurs in association with various brachiopod (*Schuchertella*?) bands. *Stictoporella excellens* occurs abundantly in the top of the Ellis Bay formation in fine calcarenite. It reappears in the lower part of the Jupiter formation and is abundant in the upper part of this formation.

In the Becscie formation, *Phaenopora superba*, a later species related to *Ptilodictya denticulata*, is abundant and the distinctive bryozoan species of the formation. It occurs in crystalline limestone throughout the formation and reappears in zones 3 and 4, Gun River formation.

In the Jupiter formation, *Ptilodictya sulcata* and *P. ensiformis* are common in the lower part of the formation and are abundant near the top. *Stictoporella excellens* likewise is abundant near the top of the formation.

In the Chicotte formation, the cryptostome Bryozoa include *Ptilodictya sulcata*, *P. ensiformis*, and *Pachydictya* n. sp.

In the Ordovician rocks. Twenhofel (1928) found that the Anticosti species extended through a greater thickness of rocks than do similar species in the Richmond group, Ohio. He interpreted this phenomenon as indicating additional Ordovician time not represented in the standard Cincinnatian section. Reconsideration of the ranges of the species and the rock types in the Anticosti sequence suggests that greater deposition in a calcareous muddy facies occurred in the Anticosti area than on the continental shelf of the Cincinnati area. Comparison of faunas from the Richmond group, Ohio, and those from the English Head, Vaureal, and Ellis Bay formations suggests equivalent stratigraphic facies of the same age. On Anticosti Island the thick sequence of well sorted clastic limestones of various grain size has alternatively rocks of either finely comminuted calcite or recrystallized calcite matrices cementing assemblages of fragmented fossils. Shell hashes having crinoid columnals, brachiopods, solitary corals, ostracods, trilobites, and bryozoans generally alternate with sparsely fossil-

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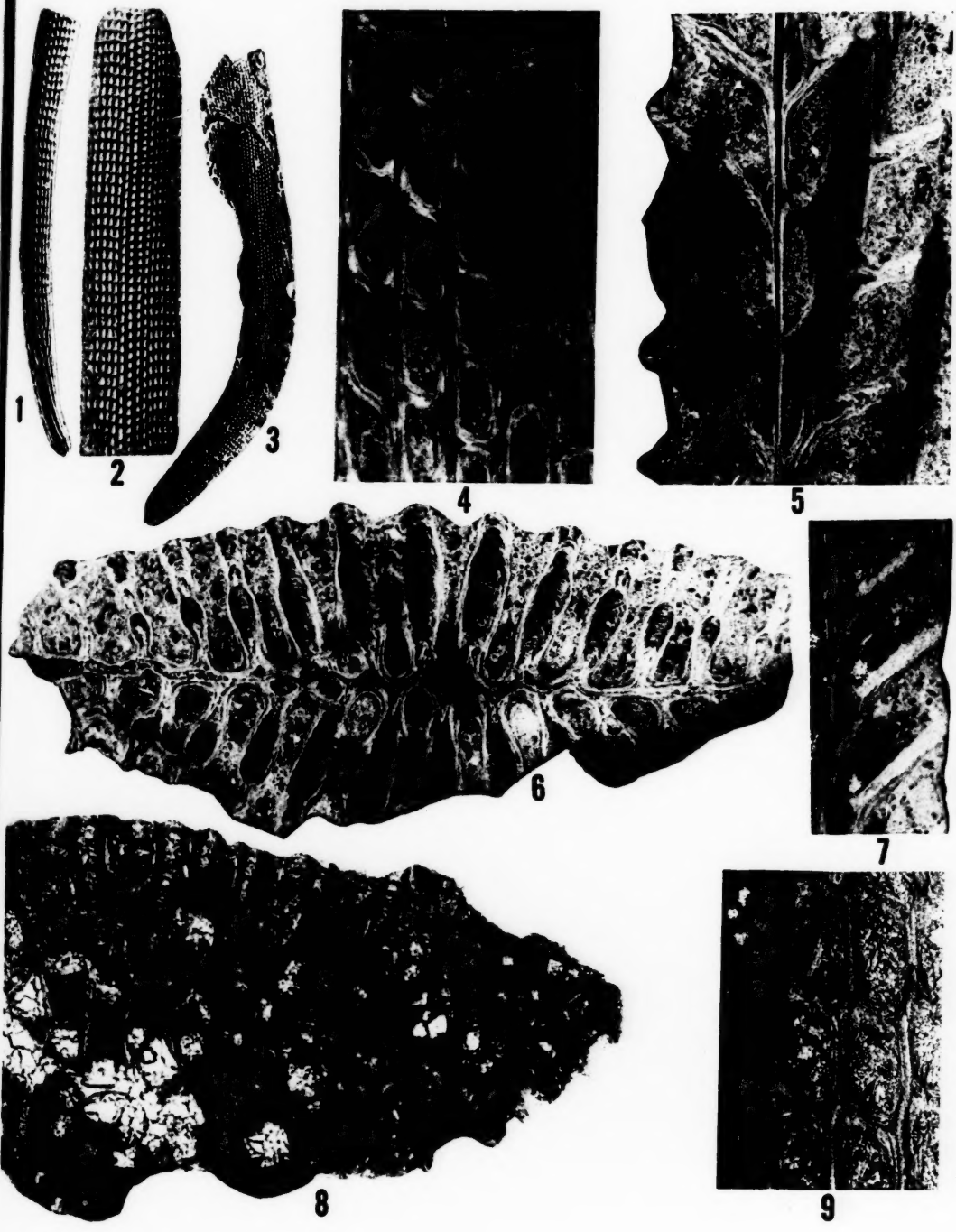
EXPLANATION OF PLATE 125

FIGS. *1–9*—*Ptilodictya sulcata* Billings. *1*, External view of a colony with pointed proximal tip. YPM 20475. East Cliff. Jupiter formation. ×5. *2*, External view of a colony with well defined longitudinal ranges of zooecia in median and lateral regions. USNM 143039. Hannah Cliffs. Gun River formation. ×5. *3*, External view of the lectotype. GSC 2501. The Jumpers. Jupiter formation. ×2. *4*, Tangential section showing zooecia in longitudinal ranges. Zooecia in the median part of the colony are on the right and those in the lateral part are on the left. USNM 143039. Hannah Cliffs. Gun River formation. ×50. *5*, Longitudinal section passing in part down the plane of the zooecial walls. Note the broadly curved laminae of the zooecial walls in the mature region. USNM 143039. Hannah Cliffs. Gun River formation. ×50. *6*, Transverse section across a colony showing a simple mesotheca and broadly curved laminate zooecial walls. Note the laminae in the mesotheca in its lateral region. USNM 143039. Hannah Cliffs. Gun River formation. ×50. *7*, Longitudinal section of a colony showing well developed superior hemisepta at the base of the mature region. USNM 143040. Jupiter River. Jupiter formation. ×50. *8*, Transverse section cut from the lectotype. GSC 2501. The Jumpers. Jupiter formation. ×50. *9*, Tangential section cut from the lectotype in the lateral part of the colony. Note the finely pustulous zooecial walls. GSC 2501. The Jumpers. Jupiter formation. ×50.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iferous calcilutite. This suggests frequent redistribution of the benthonic and planktonic forms possibly by mass movement down the continental slope as the basin of deposition rapidly subsided.

The fauna from the English Head, Vaureal, and Ellis Bay formations contains many forms closely related to those of the Richmond group, Ohio, and the Maquoketa shale, Iowa. The bryozoans *Sceptropora facula* (Whitewater member, Richmond group) and *Ptilodictya denticulata* are abundant in the English Head, and Vaureal formations. Likewise the ostracod *Primitia? lativia* (Whitewater member, Richmond group) is recorded from the English Head formation. The stromatoporoid *Beatricea* (Liberty member, Richmond group) is present in the Vaureal and Ellis Bay formations. The graptolite *Climacograptus putillus* (Maquoketa shale) is recorded from the English Head and Vaureal formations. In addition, the tabulate coral *Calapoecia* from the English Head, Vaureal and Ellis Bay formations, the brachiopod *Catazyga* from the English Head and Vaureal formations, the cephalopod *Characteroceras* from the English Head and Vaureal formations and the ostracod *Tetradella* from the English Head and Vaureal formations are typical North American late Cincinnatian (Richmond) genera. In discussing the correlation of the Ordovician cephalopods from Baffin Island and the District of Franklin, Northwest Territories, Miller, Youngquist & Collinson, (1954) and Sweet & Miller (1958) noted their close similarity to those from Anticosti Island, They believed that the Ordovician cephalopods of the far north suggested an early Cincinnatian (Eden or Maysville) age but noted that Richmond affinities were indicated by various forms.

Comparison of the Silurian faunas is extremely difficult and this section of the Anticosti sequence requires extensive revision before relations between other faunal provinces may be established. The graptolite and shelly faunas are from different lithofacies and offer comparison with faunas in other areas. However there are few links for correlating between these lithofacies. Anticosti species of graptolites are compared with the standard British sequence as the graptolite sequence in North America is incompletely known. Diplograptids such as *Climacograptus typicalis* are recorded from as high as the lower half of the Jupiter formation. In Great Britain such diplograptid types extend into the Llandovery (Bulman, 1958). Also the graptolite association of *Retiolites geinitzianus* and *Monograptus priodon*?, having distally isolate, hooked thecae with spines, from the lower and middle parts of the Jupiter formation, suggests an age equivalent to upper Llandovery. Thus the boundary equivalent to that of the Llandovery—Wenlock appears to lie within the Jupiter formation.

Little is known of the fauna of the lower part of the Silurian calcareous facies in

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EXPLANATION OF PLATE 126

FIGS. *1–3*—*Ptilodictya canadensis* Billings. *1*, View across the mesothecal plane of the holotype. GSC. 2005. Carleton Point. English Head formation. ×2. *2*, Deep tangential section of part of the colony. The three longitudinal ranges on the left are in the lateral region of the colony and the three on the right are in the median region. GSC 2005. Carleton Point. English Head formation. ×50. *3*, External view of part of a colony with well defined median and lateral regions. USNM 143041. Chaloupe Cliff. Jupiter formation. ×5.

4–6—*Ptilodictya ensiformis* (Hall). *4*, External view of the holotype. AMNH 1498. Flamborough Head, Ontario, Canada. Cataract group. ×5. *5*, Deep tangential section across the colony. Note the slender zooecial walls. YPM 20399. East Cliff. Jupiter formation. ×50. *6*, Transverse section across a colony. Note the slender mesothecal plane and zooecial walls. YPM 20398. Cape Henry. Vaureal formation. ×50.

7,8—*Ptilodictya whiteavesi* Ulrich. *7*, Longitudinal section cut from the holotype and illustrated by Ulrich, 1889. Note the superior hemiseptum at the base of the mature region of the long zooecial tube. USNM 153048. Stony Mountain, Manitoba, Canada; Stony Mountain formation. ×50. *8*, Tangential section cut from the holotype with median longitudinal ranges on the left and lateral longitudinal ranges on the right. USNM 143048. Stony Mountain, Manitoba, Canada; Stony Mountain formation. ×50.

northeastern United States. No detailed paleontological study is available on the Alexandrian Series, Illinois, and the very impoverished fauna of the sandstone facies of the New York and Ontario area permits little comparison with the Anticosti Island fauna. Species of the genus *Phaenopora*, common in the Becscie and Gun River formations, and the lower part of the Cararact group of Ontario, are also found in the calcareous facies of the Siberian platform (Astrova, 1955). In Russia the genus has only a few representatives in strata equivalent to the upper Caradoc and becomes abundant in lower Llandovery equivalents and reappears in lower Wenlock equivalents.

In the middle Silurian, the ostracod zones as recognized in Maryland (Ulrich & Bassler, 1923) and New York State (Gillette, 1947; Bolton, 1957) offer limited correlation with the Anticosti Island fauna. *Zygobolba excavata* in the lower part of the Jupiter formation suggests correlation with the middle part of the Lower Clinton, New York State. *Zygobolba decora* in the upper part of the Jupiter formation suggests correlation with the upper part of the Lower Clinton. However the brachiopod, *Eospirifer radiatus*, ranging through the Jupiter and Chicotte formations, suggests correlation with the Upper Clinton.

SYSTEMATIC PALEONTOLOGY

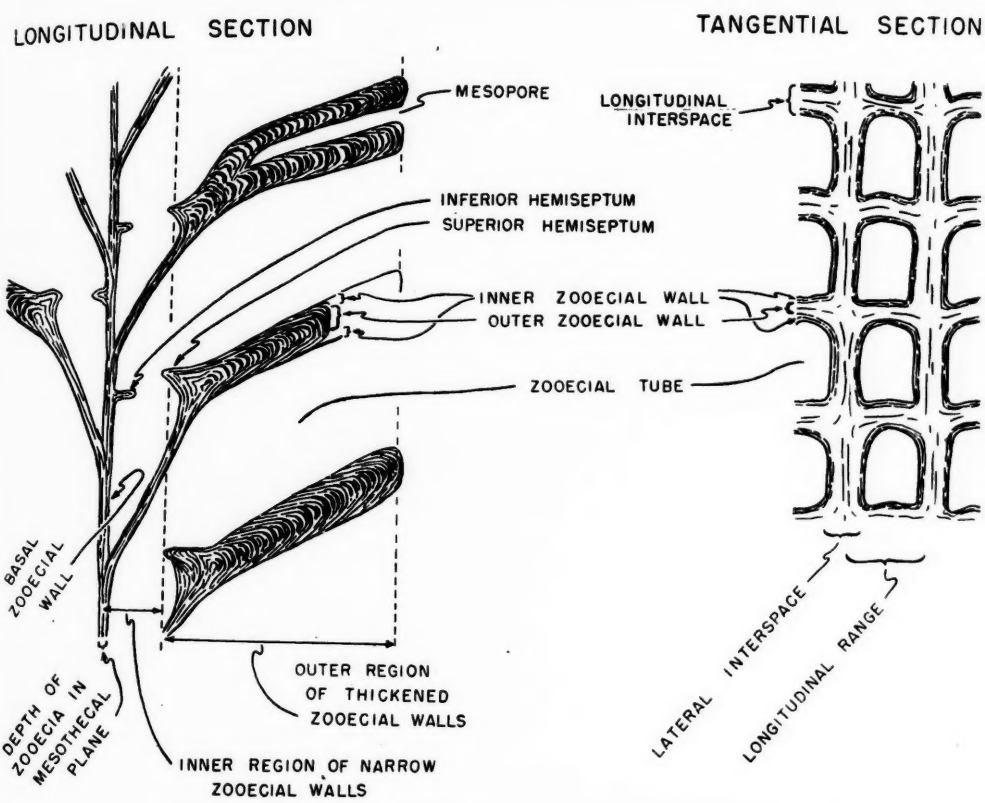
In the generally accepted classification (Bassler, 1953) the genera referred to in Table 1 are assigned to three families: *Ptilodictya* and *Phaenopora* to the Ptilodictyidae, *Stictoporella* and *Stictopora* to the Stictoporellidae, and *Pachydictya* to the Rhinidictyidae. Based on restudy and reevaluation of the primary types of these genera they are regrouped into categories informally named by Phillips (1960a) escharoporid, stictoporid, and pachydictyid: *Ptilodictya*, *Phaenopora*, and *Stictoporella* are assigned to the escharoporid group; *Stictopora* to the stictoporid group; and *Pachydictya* to the pachydictyid group. The morphology of these bifoliate genera is described in Phillips (1960) and Ross (1960).

INTERPRETATION OF SKELETAL STRUCTURES

The skeletal walls of genera belonging to the informally named categories are composed of laminate calcite which is also found in the Fenestellidae, Rhabdomesidae, many of the trepostomes, and the Recent Heteroporidae. As in the Recent Heteroporidae which deposit their laminate calcite at the base of the ectodermal tissue lining the zooids, the steeply inclined laminae of the inner zooecial walls of the Paleozoic cryptostomes herein described indicate the extent that cellular tissue lined the zooids. These steeply inclined laminae of the inner zooecial walls (Text-fig. 2) intertongue with the broad distally convex laminae of the outer zooecial walls suggesting that the cellular tissue that lined the zooids extended from one zooecium to the next. Thus the walls appear to have developed by continuous deposition of calcite along the inner walls of the zooids and across the region between the zooids as the zooids moved forward (distally) with the growth of the colony.

Superior hemisepta at the base of the outer zone of thickened walls have laminae of the inner zooecial walls. Seemingly the superior hemisepta first appear as the individual zooids diverge out of the region of restricted space near the mesothecal plane and it is here also that the zooecial walls thicken appreciably. As the zooids grow distally, laminae of the inner zooecial walls are continuously deposited and the superior hemisepta are extended as projections into the zooecial tubes. Likewise the inferior hemisepta are lengthened by a similar process. At what stage the inferior hemisepta first develop in the laminae of the zooecial walls near the mesothecal plane is not known. Diaphragms with laminae curving into the inner zooecial walls were apparently deposited by tissue lining both sides of the structure but the main part of the deposition appears to be on the distal side. Perforations through the mesothecal plane lined with laminae which are continuous with those lining the inner zooecial walls also suggest that tissue lined the zooids in their inner regions and apparently lined the perforations through the mesothecal plane.

The informal categories stictoporid, escharoporid, and pachydictyid are characterised by colonies in which the zooecia are aligned in longitudinal ranges. Deep



TEXT-FIG. 2—Diagrammatic sketches of zoarial micro-structures observed in longitudinal and tangential sections as discussed in this paper. ×75 approx.

tangential sections of the colonies illustrate this feature exceedingly clearly. In tangential sections cutting the outer region of colonies the walls which form the short longitudinal interspaces and the long lateral interspaces are composed of broad laminae of the outer zooecial walls and concentric laminae of the inner zooecial walls which form a narrow zone at the edges of the zooecial tubes. In deep tangential sections cutting the inner region of colonies the walls which form the short longitudinal interspaces and the long lateral interspaces are composed of narrow bands of laminate calcite. In exceedingly deep tangential sections cutting the mesothecal plane the basal zooecial walls lying parallel to the mesothecal plane appear as narrow amalgamate bands of calcite. Median tubuli when present emphasise this structure, which then appears to be composed of numerous parallel short bars oriented longitudinally. Budding in the colonies takes place in the distal part of each range with the new zooecia beginning in the mesothecal plane. Longitudinally within each range the basal zooecial walls overlap in the limited space afforded in the region of the mesothecal plane but the overall sequence of budding between the various ranges across the mesothecal plane remains conjectural.

ESCHAROPORID GROUP

Colonies are bifoliate and have ribbon-shaped or explanate forms of growth. Zooecia are aligned in longitudinal ranges. Mesopores occur in the interspaces (*i.e.*, the zooecial walls) separating the zooecial tubes. Acanthopores are absent.

Zooecia grow from the mesothecal plane

at a low angle and form a narrow inner region of thin zooecial walls. The base of the superior hemisepta marks the beginning of the outer region of thickened zooecial walls. The inner zooecial walls lining the zooecial tubes have laminae steeply inclined distally to the surface of the colony. The laminae of the inner walls pass into the broadly curved convex intertonguing laminae of the outer walls.

The mesothecal plane lacks median tubuli.

Genus PTILODICTYA Lonsdale

Ptilodictya LONSDALE, *in* Murchison, 1839, Silurian System, p. 676.

Type species: *Ptilodictya lanceolata* (Goldfuss), 1829, Petrefacta Germaniae, v. 1, p. 104, pl. 37, figs. 2a,b,c,d.

Emended definition.—Colonies are bifoliate and have ribbon-shaped or explanate forms of growth. They grow from pointed proximal tips. Zooecia at the surfaces of the colonies are aligned in longitudinal ranges which are demarcated by slightly raised zooecial walls of the lateral interspaces. Mesopores and acanthopores are lacking.

Zooecia grow from the mesothecal plane at a low angle and form a narrow inner region. Thickening of the zooecial walls at the bases of the superior hemisepta marks the beginning of the outer region of the zooecia. The thickened zooecial walls of this outer region have a curved laminate microstructure. The inner zooecial walls lining the zooecial tubes have laminae steeply inclined distally to the surface of the colony. These laminae of the inner walls pass into the broadly curved convex intertonguing laminae of the outer walls. The outer walls are not separated by zooecial boundaries and appear amalgamate.

Superior hemisepta also have a laminate microstructure which is continuous with the microstructure of the inner zooecial walls. Inferior hemisepta, generally short spines projecting from the mesothecal plane and beneath the superior hemisepta, also have a laminate microstructure which is continuous with the laminae of the mesothecal plane.

The mesothecal plane lacks median tubuli. It is composed of the overlapping basal zooecial walls.

Remarks.—The longitudinal ranges in *Ptilodictya* are generally separable into two kinds: median longitudinal ranges which extend along the median part of a strap and contain zooecia opening orthogonally to the surface; and lateral longitudinal ranges which lie on each side of the median longitudinal ranges and contain zooecia opening obliquely to the surface.

Some species grow to sizable lengths; specimens of the type species, *P. lanceolata*, may be 12 cm. long. The Anticosti Island sequence contains one species, *P. ensiformis*, which is smaller than is usual for the genus. It has previously been identified as *Ptilodictya flagellum* Nicholson, 1875, from Cincinnati, Ohio, and *P. gladiola* Billings, 1866, from Anticosti Island. Although the type material for these two species has not been located it appears they are synonyms of *P. ensiformis* (Hall) 1852.

The type material of the species *Ptilodictya alcyone* Billings, 1866, *P. arguta* Billings, 1866, and *P. rustica* Billings, 1866, from Anticosti Island has been examined externally. As these small fragments in the type collections are not sufficient for sectioning to determine the skeletal microstructures, the three species are at present not recognizable.

PTILODICTYA CANADENSIS Billings
Pl. 126, figs. 1–3

Ptilodictya canadensis BILLINGS, 1866, Catalogue of the Silurian Fossils of the Island of Anticosti, p. 9,10; BASSLER, *in* Twenhofel, 1928, Geology of Anticosti Island, Canada Geol. Survey Mem. 154, p. 161, pl. 7, fig. 19; pl. 9, fig. 9.

?Ptilodictya whiteavesi ULRICH, 1889, Canadian Geol. Survey Contr. to Micro-paleontology of the Cambro-Silurian rocks of Canada, pt. 2, p. 44,45, pl. 8, figs. 1,1a–1c.

Type material.—Holotype GSC 2005. Collected by James Richardson from Carleton Point, Anticosti Island, English Head formation, Ordovician.

Additional material.—Five specimens from Ordovician and Silurian rocks, Anticosti Island.

Description.—Colonies are very broad nonbifurcate straps with pointed proximal tips (Pl. 126, figs. 1,3). In most specimens, including the holotype, the zoarial fragments are split along the mesothecal plane. Monticules consisting of unusually large zo-

oecial tubes and thickened zooecial walls may be present as in USNM 79504 and 79516. When present they tend to disrupt the regular arrangement of the zooecia in longitudinal ranges. These ranges, as in *Ptilodictya sulcata*, are separable into median and lateral ones.

Longitudinal and transverse sections of zoarial fragments show the characteristic ptilodictyid skeletal microstructures of the zooecial tubes and laminate zooecial walls as discussed under *Ptilodictya sulcata*. The thick zooecial walls are composed of the steeply sloping inner walls and broadly curved outer walls.

In tangential sections the zooecia have an elliptical or quadrangular cross section and the major axis of the ellipse is in the direction of growth of the colonies (Pl. 126, fig. 2).

The simple mesothecal plane lacks medien tubuli.

Occurrence:

English Head Formation:
Zone 3. USNM cat. no. 79504.
Zone 4. USNM cat. no. 79516, GSC 2005.
Gun River formation:
Zone 3. USNM cat. no. 143039.
Jupiter formation:
Zone 8–9. USNM cat. no. 143041.

Age.—Late Ordovician to middle Silurian.

Remarks.—When more material becomes available a more adequate description can be made of *P. canadensis*. The very broad zoarial strap with numerous median and lateral longitudinal ranges distinguishes *P. canadensis* from P. *sulcata*.

Ptilodictya canadensis, although not common in the Anticosti Island sequence, is associated with brachiopods, trilobites, crinoid columnals, and bryozoans such as *P. sulcata* in medium grey calcilutite beds.

Ptilodictya whiteavesi Ulrich (1889), described from the Ordovician rocks of Stony Mountain, Manitoba, Canada, may be a synonym of *P. canadensis* but insufficient data about either species do not permit adequate comparison.

The handspecimen of the holotype of *Ptilodictya whiteavesi*, collected by T. C. Weston and A. McCharles, 1884, has been examined and those thin sections cut from the holotype by Ulrich, housed in the U. S. National Museum (USNM cat. no. 143048), have been studied. Portions of the longitudinal and tangential sections of the type material are illustrated on Pl. 126, figs, 7,8. All the dimensions of *P. whiteavesi* lie within the range of the dimensions of *P. canadensis*. Both species have similar morphological features and show monticules developed across the broad colonial straps which have well developed median and lateral longi-

TABLE 2—MEASUREMENTS OF *Ptilodictya canadensis* BILLINGS (in millimeters)

Measurements (mm.)	GSC 2005	USNM 79516	USNM 79504	USNM 143041	USNM 79510–3
Zoarial branch length	82	12	12	13	23
Zoarial branch width	10–11	minimum 6	minimum 12	13	7.8
Zoarial branch depth	not det.	1.6	2.0	.7	approx. 1.3
Ranges on branch	49	minimum 22	minimum 43	55	approx. 48
No. of median ranges	8	approx. 10	not det.	15	not det.
No. of zooecia/2 mm. Longitudinally	5–5.5	6	approx. 7	5–6.5	median 7 lateral 7.5–8
Laterally	12	9	7	8	median 10 lateral 9
Longitudinal interspace	.02–.08	.09–.12	.12	.05–.08	median .07–.08 lateral .04–.08
Lateral interspace	.04–.06	.12–.14	.12	.04–.07	median .10–.11 lateral .06–.08
Diameter of zooecia at surface	(.30–.44)×(.09–.14)	(.18–.20)×(.08–.10)	(.24–.32)×(.19–.26)	(.26–.38)×(.10–.14)	median (.16–.18)×(.08–.09) lateral (.20–.23)×(.12–.18)
Depth of zooecia in mesotheca	not det.	.02	.03	.03	not det.

TABLE 3.—MEASUREMENTS OF TYPE MATERIAL OF *Ptilodictya whiteavesi* ULRICH USNM 143048 (in millimeters)

Zoarial branch length	not determined
Zoarial branch width	9.0
Zoarial branch depth	incomplete 1.46
Ranges on branch	minimum 33
No. of median ranges	10
No. of zooecia/2 mm.	
Longitudinally:	
Median	6
Lateral	5.5
Laterally:	
Median	10
Lateral	6
Longitudinal interspace	
Median	.06–.08
Lateral	.08–.10
Lateral interspace	
Median	.10–.12
Lateral	.07–.12
Dia. of zooecia at surface	
Distally:	
Median	(.24–.28)× (.06–.08)
Lateral	(.20–.28)× (.16–.30)
Depth of zooecia in mesotheca	.02
Ratio: Width, outer zone of thickened walls / Width of zooecium	0.85

tudinal ranges. In tangential section the zooecial cross section is quadrangular in the median portions and quadrangular to hexagonal in the lateral regions. Superior hemisepta, one per zooecium, lie at the base of the outer zone of the thickened zooecial walls but do not extend completely across the zooecial tube. Narrow, flat diaphragms, generally one per zooecial tube, occur in the outer part of the zooecial tube. A very occasional small mesopore seems to be present at the junction of zooecial walls in the lateral regions.

Ulrich's illustration (1889, pl. 8, fig. 1c) of a longitudinal section of *Ptilodictya whiteavesi* is misleading, as the inner zooecial walls are not barbed with a series of short spines. In thick sections the dark matrix between calcite boundaries might suggest such structures.

PTILODICTYA DENTICULATA
Ross, n. sp.
Pl. 127, figs. 1-7

Type material.—Holotype 143044; Baie Ste. Claire, Anticosti Island; English Head formation, upper Ordovician.

Additional material.—15 zoarial fragments from various localities in the Ordovician, Anticosti Island.

Description.—Broad, bifoliate and explanate colonies grow from pointed proximal tips. The surfaces of the colonies consist of elevated monticules and regularly arranged zooecia between these tubercles (Pl. 127, fig. 4). Zooecia are not arranged in longitudinal ranges but they seem to lie in an intersecting diagonal pattern. Mesopores and acanthopores are absent.

Zooecia grow at a low angle from the mesothecal plane as thin walled partitions and form a narrow inner zone. The outer zone of thickened zooecial walls is much wider and begins at the base of the superior hemisepta (Pl. 127, fig. 5). The thickened zooecial walls consist of steep, distally sloping laminae of the inner walls which pass into the broad convexly curved intertonguing laminae of the outer wall (Pl. 127, figs. 2,3). The microstructure of the zooecial walls is thus the same as that in other species of *Ptilodictya*. Numerous small denticles, regularly arranged in a longitudinal pattern down the inner walls project into the zooecial tubes (Pl. 127, figs. 2,3), and are similar to the longitudinally arranged denticles observed in the skeletal microstructure of *Phaenopora superba* Billings. These toothlike projections develop in the laminae of the inner zooecial walls. Diaphragms are not present in the zooecial tubes.

Shallow tangential sections across the surface of colonies show quadrate and oval zooecia in cross section (Pl. 127, fig. 1). The narrow laminate bands of the inner zooecial walls lie on each side of the broader outer walls. Denticles appearing as small spikes in the inner zooecial walls may project into the zooecial tube. Shallow tangential sections across monticules show enlarged, irregular zooecia in cross section and greatly thickened zooecial walls (Pl. 127, fig. 1).

The simple mesotheca lacks median tubuli. However small perforations across

the mesotheca may be present (Pl. 127, fig. 7). These openings which connect zooecial tubes on opposite sides of the mesotheca are lined with laminae which are continuous with those lining the inner zooecial walls. These laminae may infill part or the entire opening in the mesotheca.

Occurrence:

English Head Formation
Zone 2. USNM cat. no. 143046.
Zone 4. YPM coll. no. 3019/9;-YPM coll. no. 3019/7—YPM cat. no. 20823; YPM cat. no. 20822; USNM cat. nos. 143042 to 143045.

Age.—Late Ordovician.

Remarks.—This distinctive species is characteristic of the English Head formation. It is distinguished by its tuberculate explanate growth and lack of median and lateral longitudinal ranges from *Ptilodictya canadensis.*

Its form of growth is similar to that of *Phaenopora* Billings, which is probably a related younger species in the Silurian and in which mesopores are abundant in the outer zooecial walls. The skeletal microstructure of both species is very similar and they differ in the presence or absence of mesopores and are placed in different genera on this basis.

Ptilodictya magnifica Miller 1878, from the Cincinnatian, Cincinnati, Ohio, appears to belong in the *Ptilodictya denticulata-Phaenopora superba* lineage. Mesopores are sparsely developed and occur generally in the elevated monticules of *P. magnifica.*

Ptilodictya denticulata is associated with ostracods, crinoid columnals, algae, solitary corals, and brachiopods in well sorted siliceous calcarenite beds.

The species name *denticulata* (Latin) refers to the denticulate inner zooecial walls commonly found in its colonies.

PTILODICTYA ENSIFORMIS (Hall)
Pl. 126, figs. 4–6

Phaenopora ensiformis HALL, 1852, Paleontology of New York, v. 2, p. 48, pl. 16, figs. 8a–8c.
Ptilodictya ensiformis (HALL), ULRICH, 1882, Jour. Cincinnati Soc. Nat. Hist., v. 5, p. 172; WHITFIELD & HOVEY, 1899, Am. Mus. Nat. Hist. Bull. 11, p. 108.
?Ptilodictya gladiola BILLINGS, 1866, Catalogue of the Silurian Fossils of the Island of Anticosti, p. 10.

Type material.—Holotype AMNH 1498. Flamborough Head, Ontario, Canada; Cataract group, Silurian.

Additional material.—About 40 zoarial fragments from various localities in the Ordovician and Silurian rocks of Anticosti Island.

Description.—Colonies are exceptionally slender unbranched bifoliate stems which grow from pointed proximal tips. Zooecia

TABLE 4—MEASUREMENTS OF *Ptilodictya denticulata* ROSS, n. sp.

Measurements (mm.)	Holotype USNM 143044	YPM 20822	YPM 20823
Zoarial branch depth	2.2	1.1–2.8	3.0–3.2
No. of zooecia/2 mm. Longitudinally	9	8	8
Laterally	10	8.5–9	8–11
Longitudinal interspace	.06–.08	.08–.11	.10
Lateral interspace	.06	.08–.10	.06–.08
Diameter of zooecia at surface of colony	(.14–.20)× (.11–.14)	(.15–.20)× (.10–.15)	(.12–.18)× (.10–.15)
Depth of zooecia in mesotheca	.01–.02	.02	.05
Ratio: Width of outer zone of thickened walls / Width of zooecium	.80–.86	approx. .75	.87

are regularly arranged in median and lateral longitudinal ranges and mesopores and acanthopores are lacking.

Being very slender, colonies are difficult to section and the small zoarial fragment of the holotype was not sectioned as there was insufficient material to make thin sections and to retain part of the colony as a hand-specimen. Tangential sections (Pl. 126, fig. 5) reveal zooecial tubes which are quadrangular in cross section and slender laminate zooecial walls. In transverse section the narrow mesotheca lacks median tubuli and the thickened zooecial walls near the periphery display broadly curved laminate zooecial walls. Longitudinal sections show the characteristic ptilodictyid zooecial tubes and the laminate zooecial walls as discussed under *Ptilodictya sulcata*.

Occurrence:

English Head Formation:
Zone 5? YPM (Twenhofel 59)
Vaureal formation:
Zone 3–4. YPM coll. no. 3063/31—YPM cat. no. 20398.
Ellis Bay formation:
Zone 2. YPM (Twenhofel 1313), YPM 3063/34—YPM cat. no. 20400.
Zone 7. YPM coll. nos. 3063/41–3063/60, 3063/58—YPM cat. no. 20819.
Zone 10. YPM (Twenhofel 1227); YPM (Twenhofel 47)—YPM cat. no. 20820.
Jupiter formation:
Zone 1. YPM (Twenhofel 1755); YPM 1391/1755.
Zone 2. YPM (Twenhofel 39).
Zone 4. YPM (Twenhofel 45); YPM (Twenhofel 109); YPM (Twenhofel 717)—YPM cat. no. 20399; YPM coll. no 3063/75; YPM (Twenhofel 14); YPM coll. no. 3063/76—YPM cat. no. 20821; YPM coll. nos. 3063/77, 3063/78, 3063/118.
Zone 7. YPM (Twenhofel 799).
Zone 9. YPM (Twenhofel 42); YPM (Twenhofel 1397).
Zone 10. YPM (Twenhofel 50); YPM coll. no. 3063/92.

Age.—Late Ordovician to middle Silurian.

Remarks.—As the holotype of this species occurs in lower Silurian dolomite of the Cataract group, Ontario, Canada, the poor preservation of the type material does not permit adequate description of the species.

The very slender dimensions of the colonies of *Ptilodictya ensiformis* distinguish it from the more strongly developed colonies of *P. sulcata*. *P. ensiformis* has a greater number of zooecia per 2 mm. laterally, and narrower longitudinal and lateral interspaces than *P. sulcata*.

Most of the zoarial fragments having two mesopores in the longitudinal interspace which Bassler (1928) referred to *Phaenopora ensiformis* belong to *Stictoporella excellens* (Billings).

Long zoarial fragments of *P. ensiformis* are commonly draped across broad, costellate brachiopods in thin calcarenite bands or shell hashes intercalated between calcilutite. Likewise they are commonly associated with abundant *Helopora* spp. and *Nematopora* spp. or with numerous ostra-

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EXPLANATION OF PLATE 127

FIGS. *1–7*—*Ptilodictya denticulata* Ross, n. sp. *1*, Shallow tangential section showing zooecial walls indented by denticles. USNM 143042. Wreck Point near Highcliff Point. English Head formation. ×50. *2*, Portion of a transverse section showing broadly curved laminae of the zooecial walls which develop at the base of the mature region. The denticles, also consisting of laminae, line the inner zooecial walls. USNM 143043. Baie Ste. Claire. English Head formation. ×100. *3*, Portion of a transverse section of the holotype showing a simple mesotheca and denticles projecting into the zooecial tubes. Note the superior hemiseptum at the base of the mature region. USNM 143044. Baie Ste. Claire. English Head formation. ×50. *4*, External view of part of the holotype showing elevated monticules and zooecia. USNM 143044. Baie Ste. Claire. English Head formation. ×10. *5*, Transverse section of part of a colony with elevated monticules. USNM 143045. Baie Ste. Claire. English Head formation. ×5. *6*, Shallow tangential section cut across a monticule. Note the irregular zooecia and denticles. USNM 143046. Dry Point. English Head formation. ×50. *7*, Portion of a transverse section cut from the holotype showing a number of pores in the mesotheca. These pores are lined with laminae continuous along the inner zooecial walls. USNM 143044. Baie St. Claire. English Head formation. ×100.

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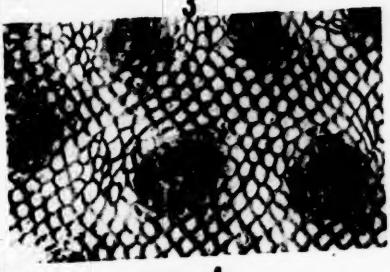

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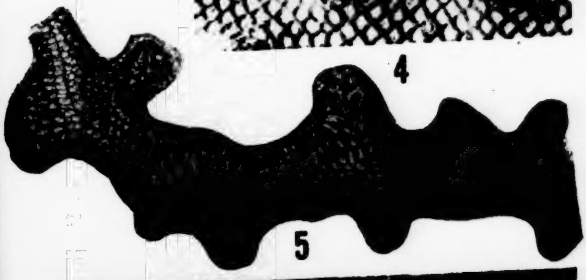

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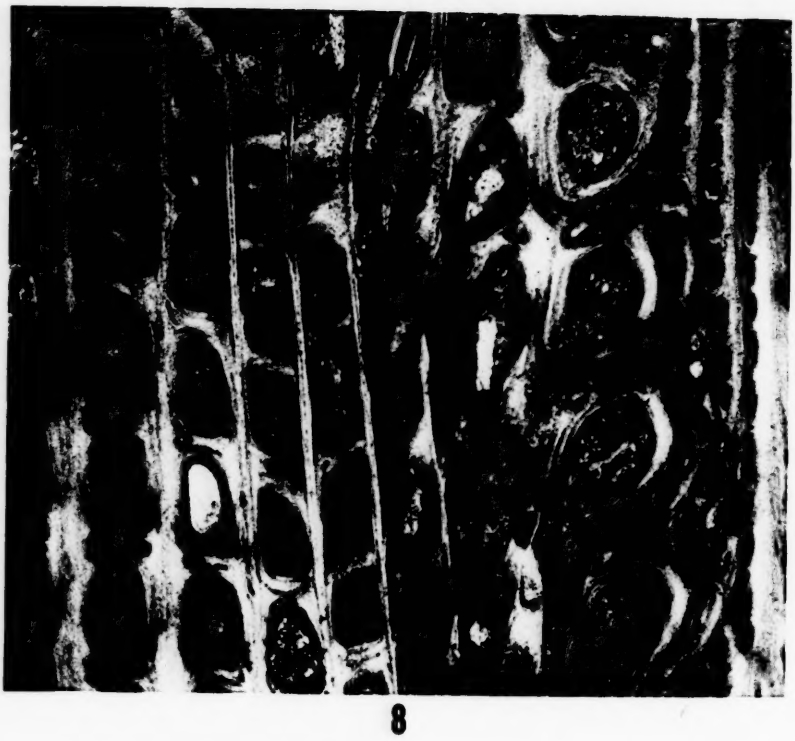
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TABLE 5—MEASUREMENTS OF *Ptilodictya ensiformis* (HALL)

Measurements (mm.)	YPM 20819	YPM 20398	YPM 20820	YPM 20821
Zoarial branch length	14.5	8	13.5	14.
Zoarial branch width	.6	1.0	1.5	1.0
Zoarial branch depth	.36	.30	.38	.56
Ranges on branch	5	8	9	5
No. of zooecia/2 mm.				
Longitudinally	8	median 7	7–8	5.5–7
Laterally	16	18	13	13
Longitudinal interspace	.03	.01–.02	.04	.03–.04
Lateral interspace	.04	.01–.02	.05–.06	.03–.07
Diameter of zooecia at surface	(.18–.26)× (.07–.10)	(.26–.28)× (.09–.10)	(.20–.28)× (.08–.10)	(.24–.30)× (.10–.13)
Depth of zooecia in mesotheca—mm.	.02	.01	.02	.03
Ratio: Width of outer zone of thickened walls / Width of zooecium	not det.	not det.	.75	.75

cods. Trilobites and crinoid columnals comprise a small percent of the shell fragments.

The type material of *Ptilodictya gladiola* Billings (1866) was illustrated by Bassler (1928) for the first time but has not been located by the writer and is presumed missing. The species appears very similar to *Ptilodictya ensiformis* (Hall) (1852) and is placed with question in synonomy with it.

PTILODICTYA SULCATA Billings
Pl. 125, figs. 1–9

Ptilodictya sulcata BILLINGS, 1866, Catalogue of the Silurian fossils of the Island of Anticosti, p. 35; BASSLER, *in* Twenhofel, 1928, Geology of Anticosti Island, Canada Geol. Survey Mem. 154, p. 162, pl. 10, figs. 9–11.

Type material.—Lectotype GSC 2501. The lectotype and the syntype GSC 2501a were collected by James Richardson, 1856, at the Jumpers, Anticosti Island, Jupiter formation, Silurian.

Additional material.—About 50 zoarial fragments from Ordovician and Silurian rocks, Anticosti Island.

Description.—Colonies are nonbifurcate ribbon-shaped straps growing from pointed proximal tips (Pl. 125, fig. 1). Zooecia are

EXPLANATION OF PLATE 128

FIGS. *1–9—Stictoporella excellens* (Billings). *1*, External view of the holotype, GSC 2248. Ellis Bay; Ellis Bay formation. ×2. *2*, Portion of a colony with mesopores along its lateral margin. YPM 20470. Lower beds at The Jumpers. Jupiter formation. ×5. *3*, Portion of a colony growing from a pointed proximal tip. USNM 143036. East Jupiter Cliff. Jupiter formation. ×10. *4*, Slender stem of a colony with well defined longitudinal ranges of zooecia and mesopores. USNM 143037. West Ellis Bay. Ellis Bay formation. ×10. *5*, Longitudinal section showing well developed superior and inferior hemisepta at the base of the mature region. YPM 20473. Twenhofel's Vaureal River section, unit 22. Ellis Bay formation. ×50. *6*, Oblique longitudinal section showing broadly curved laminate zooecial walls in the mature region. USNM 143038. East Jupiter Cliff. Jupiter formation. ×50. *7*, Transverse section of a colony. Note the narrow mesotheca and thickened laminate zooecial walls in the mature region. YPM 20474. Bell River. Jupiter formation. ×50. *8*, Tangential section toward the lateral margin of a colony. Note the abundant mesopores in the margin and the obliquely directed zooecia. USNM 143038. East Jupiter Cliff. Jupiter formation. ×50. *9*, Tangential section across part of a colony. Two mesopores lie in the longitudinal interspace between successive zooecia. GSC 15099. Two miles east of the mouth of Jupiter River. Jupiter formation. ×50.

present in well defined longitudinal ranges which are separable into two kinds (Pl. 125, fig. 2): median longitudinal ranges which extend along the median part of a strap and contain zooecia opening orthogonally to the surface; and lateral longitudinal ranges which lie on each side of the median longitudinal ranges and contain zooecia opening obliquely to the surface. Elliptical cross sections of zooecia in median longitudinal ranges have their major axis parallel to the lateral interspaces demarcating the ranges. In the pointed proximal part of a colony lateral longitudinal ranges are not strongly differentiated, but in the more distal parts of a colony these lateral longitudinal ranges are easily distinguished in handspecimen. The dimensions of zooecia in the lateral longitudinal ranges are commonly larger than those in the corresponding median part of the colony. Monticules and maculae are lacking.

Zooecia leave the mesothecal plane at a low angle and the thin walls of the inner zone pass above the superior hemisepta into the broader outer zone having thickened zooecial walls. Zooecial walls consist of narrow inner walls and broader outer walls. Laminae of the inner walls have a steep slope distally toward the outer wall and curve into the very low convexly curved inter-tonguing laminae of the outer wall (Pl. 125, fig. 6). Thus the zooecial tubes and zooecial walls have the characteristic skeletal microstructure of a ptilodictyid (Pl. 125, figs. 5–7).

Inferior and superior hemisepta are well developed in the lectotype and many specimens examined. Specimens included in this species show several interesting variations in their skeletal microstructure. For example in the zoarial fragment USNM 97193-1 from the English Head formation, two short superior hemisepta are present; one is located at the base of the thickened outer zone and the other projects from about a third the distance along the thickened outer zone. In the zoarial fragments USNM 69096 and 69106 from the Jupiter formation, incomplete diaphragms, up to four in number, extend from the lower proximal wall across three-quarters of the diameter of the zooecial tubes and do not touch the upper distal wall. They do not occur in all zooecial tubes and may be found near or in the outer zone of the zooecial tube.

In tangential section the zooecia at the surface may be almost quadrangular in cross section (Pl. 125, fig. 4) but more commonly they are elliptical. Zooecial walls between two zooecial tubes consist of thin laminate bands of the inner zooecial walls bounding a broad outer (median) wall. In shallow tangential section a fine pustulous structure is commonly present in the zooecial walls (Pl. 125, fig. 9). In shallow tangential section the zoarial fragment USNM 69051 from the Becscie formation shows denticulate inner zooecial walls which almost completely fill the zooecial tubes.

The simple mesotheca lacks median tubuli. As it widens in its lateral extensions it develops a laminate microstructure similar to that in the outer zone of zooecial walls (Pl. 125, figs. 6,8).

Occurrence:

English Head formation:
- Zone 3. USNM cat. no. 97193, YPM coll. no. 3063/23.
- Zone 4. YPM (Twenhofel 66); USNM 69066.

Vaureal formation:
- Zone 4. YPM (Twenhofel 777).
- Zone 5–6. YPM coll. no. 3063/33.

Ellis Bay formation:
- Zone 9. USNM cat. no. 79542.

Becscie formation:
- Zone 1. YPM coll. no. 3063/62; 3063/63.
- Zone 4. USNM cat. no. 69051.

Gun River formation:
- Zone 3. USNM cat. no. 143039, 143050; YPM coll. no. 3063/98, 3063/104.

Jupiter formation:
- Zone 1. YPM (Twenhofel 67); YPM coll. no. 3063/111.
- Zone 2. YPM (Twenhofel 7420)—YPM cat. no. 20398; YPM coll. no. 3063/78.
- Zone 3. YPM coll. nos. 3063/75, 3063/76.
- Zone 4. YPM coll. nos. 3063/82, 3063/84; YPM (Twenhofel 109).
- Zone 8. USNM cat. no. 69106.
- Zone 9. YPM (Twenhofel 64); YPM coll. no. 3063/86; YPM (Twenhofel 1399); USNM cat. nos. 69096, 69086.
- Zone 10. USNM cat. nos. 143040, 69084; GSC 2501; YPM coll. no. 3063/92. YPM; (Twenhofel 50); YPM (Twenhofel 41) YPM (Twenhofel 1249).

Chicotte formation:
- Zone 1. YPM coll. no. 3063/125-3.

Age.—Late Ordovician to middle Silurian.

Remarks.—This species has affinities with *Ptilodictya lanceolata* (Goldfuss). In *P. sulcata* the zooecial walls are wider and the

TABLE 6—MEASUREMENTS OF THE BRYOZOAN SPECIES *Ptilodictya sulcata* (in millimeters)

Measurements	GSC 2501	USNM 69096	USNM 69066	USNM 69104	USNM 79510–2	USNM 143039	USNM 69084–3	USNM 69084–2	USNM 69084–1	USNM 69084–5
Zoarial branch length	27	30	5.5	19	13	17	17	20	13	12
Zoarial branch width	2.0–3.3	1.5	1.5	1.4	2.8	3.0	2.6	1.0–1.9	1.8–2.0	1.2
Zoarial branch depth	1.26	.64–.70	.78	.6–.7	0.88	1.1	0.72	0.66	.60	.70
Ranges on branch	13–21	12	÷14	8	16	18	13	9–11	11–12	10
No. of median ranges	8	2	13–14	7–8	5	3	6	3–5	4–5	1
No. of zooecia/2 mm.										
Longitudinally										
Median	not det.	7	7.5	7.5	7.5	7	7	6.5	8	4
Lateral	6–8.5	6	7.5	6.5	6	6	6.5	5.5	6	6
Laterally										
Median	not det.	11	11	10	6.5	10	7	7	12	8
Distally										
Lateral	9	9	11	10	10.5	10	10	6	11	9
Longitudinal interspace										
Distally										
Median	not det.	.04–.06	.04–.07	.04	.06	.07–.08	.03–.05	.03–.05	.02	.03–.04
Lateral	.07	.04	not det.	not det.	.06	.06–.07	.02	.04	.04	.02–.04
Lateral interspace										
Distally										
Median	not det.	.06–.08	.05–.07	.08	.06	.08–.14	.03	.03–.04	.04–.06	.02–.03
Lateral	.04–.06	.03–.05	not det.	not det.	.05–.06	.06–.10	.03–.04	.04	.03–.06	.03–.06
Diameter of zooecia at surface of colony										
Distally										
Median	not det.	(.08–.10)× (.14–.18)	.10× (.11–.18)	.09× (.20–.22)	(.08–.10)× (.14–.17)	(.14–.30)× (.06–.07)	(.10–.11)× (.20–.22)	.26×.10	(.18–.24)× (.10–.12)	.09× (.22–.28)
Lateral	(.14–.16)× (.24–.28)	(.10–.12)× (.34–.36)	.14× (.10–.26)	.09× (.22–.24)	(.18–.20)× (.06–.08)	(.22–.24)× (.04–.07)	(.28–.40)× (.14–.20)	(.26–.30)× (.14–.20)	(.20–.38×) (.12–.18)	.20× (.24–.32)
Depth of zooecia in mesotheca	.02	.02	.02	.02	.05	.06	.02	.02	.02	.04
Ratio: Width of outer zone thickened walls / Width of zooecium	not det.	approx. .73	.79	not det.	not det.	not det.	not det.	not det.	not det.	not det.

diameter of the zooecia at the surface is smaller than those in *P. lanceolata*. However, in both species the dimensions of the width and depth in the colonies lie within the same range and the number of zooecia per 2 mm. is similar. Both species show a wide range of variation, as can be seen in the table of measurements. *P. sulcata* is distinguished by its smaller dimensions and lack of monticules from *P. canadensis*.

The highly variable species, *Ptilodictya sulcata*, has a wide range of distribution and a long stratigraphic range from the upper Ordovician to the middle Silurian of Anticosti Island. It occurs in calcarenite beds having a fine calcitic matrix and shell hash which have a host of other fragmented and sorted shells. Crinoid columnals, brachiopods, trilobites, ostracods, solitary corals, tentaculitids, trepostome Bryozoa and species of *Helopora* and *Nematopora* are associated with this species of *Ptilodictya*.

Genus STICTOPORELLA Ulrich

Stictoporella ULRICH, 1882, Jour. Cincinnati Soc. Nat. Hist., v. 5, p. 152.

Type species: *Stictoporella interstincta* Ulrich, 1882, Jour. Cincinnati Soc. Nat. Hist., v. 5, p. 169, pl. 8, figs. 9,9a.

Emended Definition.—Colonies are bifoliate and have a ribbon-shaped form of growth. Zooecia at the surfaces are aligned in longitudinal ranges and are oval in cross section. Mesopores, generally two in number, occur in the longitudinal interspaces between successive zooecia of the longitudinal ranges. A single series of mesopores lines the lateral margins of the colonies. Acanthopores are absent.

Zooecia grow from the mesothecal plane at a low angle and form an inner region having thin zooecial walls. The base of the superior hemisepta marks the beginning of the outer region of thickened, laminate zooecial walls. The inner zooecial walls lining the zooecial tubes have laminae steeply inclined distally to the surfaces of the colonies. The laminae of the inner walls pass into the broadly curved convex inter-tonguing laminae of the outer zooecial walls. The outer walls are continuous and appear amalgamate and are not separated by zooecial boundaries. The inner walls lining the mesopore tubes have the same steep laminate microstructure as that in the inner zooecial walls. The laminae of these inner walls pass into the broadly curved convex intertonguing laminae of the outer walls. Superior hemisepta also have a laminate microstructure which is continuous with the microstructure of the inner zooecial walls.

The mesotheca is not pierced by median tubuli.

Remarks.—The microstructure of the thickened zooecial walls in the outer region of the zooecia of *Stictoporella* is similar to that in *Ptilodictya*, and *Escharopora*. The two mesopores located in the longitudinal interspaces between successive zooecia is a distinctive feature of the genus.

As in *Ptilodictya* and *Escharopora*, the thickened zooecial walls of *Stictoporella* commonly exhibit a fine pustulous microstructure near the surface of the colonies.

The external similarity of the zooecial surfaces of *Phaenopora* Hall 1852 and *Stictoporella* Ulrich 1882 should be noted. Species of *Stictoporella* are bifoliate, bifurcate slender stems with numerous mesopores present along the lateral margins and are primarily distinguished from *Phaenopora* on the form of the colony. The poorly preserved type material of *Phaenopora explanata* Hall, type species of *Phaenopora*, is not satisfactory for determining generic and specific characters. Comparison of the skeletal microstructures of the genera is not possible until better preserved topotype material of *P. explanata* is found. Although it is difficult to define *Phaenopora* both *Phaenopora* and *Stictoporella* are retained as distinct genera until more data are available concerning the distribution and occurrence of species in this group. It should, however, be borne in mind that *Stictoporella* and *Phaenopora* may be congeneric.

STICTOPORELLA EXCELLENS (Billings)

Pl. 128, figs. 1-9

Ptilodictya excellens BILLINGS 1886, Catalogue of the Silurian fossils of the Island of Anticosti, p. 34.

Phaenopora excellens (Billings), BASSLER, *in* Twenhofel, 1928, Geology of Anticosti Island, Canada Geol. Survey, Mem. 154, p. 163, pl. 14, figs. 10,11.

Phaenopora aperta BASSLER, 1928, *in* Twenhofel, Geology of Anticosti Island, *Ibid.*, Mem. 154, p. 165, pl. 12, fig. 3.

Type material.—Holotype GSC 2248, by Bassler, 1928, pl. 16, fig. 10. Material was collected by James Richardson, 1856

from Ellis Bay; Ellis Bay formation; upper Ordovician.

Additional material.—Thirty-six fragments of colonies in the Ordovician and Silurian rocks of Anticosti Island.

Description.—Zoarial fragments are slender branching bifoliate stems or slender stems expanding rapidly from pointed proximal tips (Pl. 128, figs. 3,4). Zooecia are in regular longitudinal ranges having two mesopores in the longitudinal interspace between zooecia. The lateral margins lack zooecia and have two or more narrow rows crowded with mesopores (Pl. 128, fig. 2,8). The outer lateral row of zooecial apertures is distally oblique (Pl. 128, fig. 8). This feature is well displayed in the holotype. Narrow longitudinal ridges separating ranges of zooecia lack acanthopores.

The very small zoarial fragment designated the holotype could not be sectioned so that the skeletal microstructures are based on topotype and plesiotype material. A zoarial fragment in the USNM collection no. 69034 is recorded as a fragment from the slab of rock containing the holotype.

A well developed superior hemiseptum is present near the base of the thickened zooecial walls. It overlies a well developed inferior hemiseptum which projects into the zooecial tube from the slender zooecial wall in the inner zone of the zooecial tube (Pl. 128, fig. 5). Both zooecia and mesopore tubes lack diaphragms. The mesopores extend from near the base of the thickened zooecial walls out to the surface of the colony.

The microstructure of the thickened zooecial walls is similar to that in *Ptilodictya*, *Escharopora*, and *Graptodictya* (Pl. 128, fig. 6). The inner walls of the zooecia are lined with laminae sloping steeply into the outer zooecial walls which in turn consist of broadly curved convex intertonguing laminae. The width of the thickened zooecial walls above the superior hemiseptum is narrow.

The simple mesotheca lacks median tubuli (Pl. 128, fig. 7).

Occurrence:

Ellis Bay formation:
Zone 10. YPM (Twenhofel 43)—YPM cat. no. 20473; USNM cat. nos. 69034, 143037, 79525, GSC 2248.
Becscie formation:
Zone 1. USNM cat. nos. 69044, 69045.
Jupiter formation:
Zone 4. USNM cat. nos 69070, 69093.
Zone 5. GSC 15099.
Zone 9. YPM coll. no. 3063/86—YPM cat. no. 20474; USNM cat. no. 79533.
Zone 10. YPM coll. no. 3063/96; YPM (Twenhofel 1519)—YPM cat. no. 20470; YPM (Twenhofel 721)—YPM cat. no. 20818; USNM cat. no. 69091.
Chicotte formation:
Zone 1. USNM cat. no. 114225.

Age.—Late Ordovician?, early to middle Silurian.

TABLE 7—MEASUREMENTS OF *Stictoporella excellens* (BILLINGS)

Measurements (mm.)	Holotype GSC 2248	YPM 20818	USNM 69045–1	USNM 79533	USNM 69093
Zoarial branch length Zoarial branch width Zoarial branch depth	15 2.0 not det.	10 1.7 not det.	6 2.6 not det.	12 2.8 0.52	18 1.8 not det.
Ranges on branch No. of median ranges	10 7–8	7 not det.	11 9	11 7–9	10 6
No. of zooecia/2 mm. Longitudinally Laterally	 5–6 10	 6½ 10	 7 9–10	 5 distally 9	 6–7½ 9
Longitudinal interspace Lateral interspace	not det. not det.	0.02 0.10–0.12	.06 .1	.01 .01	.01–.02 .08
Diameter of zooecia at zoarial surface—mm.	not det.	(.08–.14)× (.18–.22)	(.16–.20)× (.08–.1)	(.20–.30)× (.14–.20)	(.20–.30)× (.12–.16)
Mesopores/zooecium	2	2	2	2	2
Diameter of mesopores	not det.	(0.02–0.04)× (.04–1.05	(.06–.08)× (.02–.04)	(.03×.05)	0.04
Depth of zooecia in mesotheca	not det.	not det.	not det.	<.01	not det.
Ratio: Width of zooecium in thickened outer zone / Width of zooecium	not det.	not det.	not det.	0.37	not det.

Remarks.—*Stictoporella excellens* has affinities with the Cincinnatian species, *S. interstincta* Ulrich. The two species have similar zoarial dimensions in the width and depth of zoarial branches, but *S. excellens* has a greater number of zooecia per 2 mm. both longitudinally and laterally. The diameter of the zooecia at the surface of colonies is very similar in both species. *S. excellens* has a more slender outer zone of thickened zooecial walls so that its ratio : width of the outer zone of thickened walls/width of zooecium is considerably lower than that of *S. interstincta*. Morphological features in the type material of *Phaenopora aperta* Bassler (1928), Jupiter formation, Anticosti Island, are identical with those in *Stictoporella excellens* and the two species are synonymous. Little is known of the skeletal microstructures of other middle and upper Ordovician specimens from North America which are described as species of *Stictoporella*. Species of *Stictoporella* are also reported from the Ordovician of Canada and the Ordovician and Silurian of Russia.

Zoarial fragments of *S. excellens* are present in medium grey calcarenites, many of which are shell hashes cemented by a fine calcitic matrix, and across bedding plane surfaces of shell accumulation in calcilutites. Associated shell fragments are abundant crinoid stems and columnals, ribbed brachiopod shells, trilobite fragments, ostracods, and abundant Bryozoa such as *Helopora* spp., *Nematopora* spp., *Ptilodictya* spp., and *Pachydictya* n. sp.

Localities on Anticosti Island

English Head formation:
- Zone 2. USNM cat. no. 143046; Dry Point (Pt. Sèche); *Ptilodictya denticulata.*
- Zone 3. USNM cat. no. 79504; Raven's Nest (Nid de Corbeau); *Ptilodictya canadensis.* YPM coll. no. 3063/23, USNM cat. no. 97193; Raven's Nest (Nid de Corbeau); *Ptilodictya sulcata.*
- Zone 4. GSC 2005, USNM cat. no. 79516; Carleton Point; *Ptilodictya canadensis.* USNM cat. no. 143042; Wreck Point; *Ptilodictya denticulata.* YPM (D4)—YPM cat. no. 20822, YPM coll. no. 3019/7—YPM cat. no. 20823; YPM coll. no. 3019/9; USNM cat. nos. 143043, 143044, 143045; Baie Ste. Claire; *Ptilodictya denticulata* USNM cat. no. 69066; White Cliffs Cape; *Ptilodictya sulcata.*
- Zone 5. YPM (Twenhofel 59); Sand Cliff; *Ptilodictya ensiformis.*

Vaureal formation:
- Zone 4. YPM (Twenhofel 777); unit 4 of Twenhofel's Vaureal River section; *Ptilodictya sulcata.* YPM coll. no 13063/31; Harvey Point; *Ptilodictya ensiformis* (YPM cat. no. 20398), and *Pachydictya* n. sp. YPM coll. no. 3063/33; lower beds, Battery Point; *Ptilodictya sulcata.*

Ellis Bay formation:
- Zone 2. YPM coll. no. 3063/34; cliff one-half mile east of Junction Cliff; *Stictopora* sp. A (YPM cat. no. 21179); *Ptilodictya ensiformis* (YPM cat, no. 20400). YPM (Twenhofel 1313); cliffs one-half to three-quarters of one mile east of Junction Cliff; *Ptilodictya ensiformis.*
- Zone 7. YPM coll. no. 3063/41; Cape James Bay; *Ptilodictya ensiformis.* YPM coll. no. 3063/60; west side of Lousey Cove; *Ptilodictya ensiformis.*
- Zone 9. USNM cat. no. 79542; Cape Eagle; *Ptilodictya sulcata.*
- Zone 10. USNM cat. nos. 143037, 79525; west Ellis Bay; *Stictoporella excellens.* YPM (Twenhofel 43); unit 22, Vaureal River section; *Stictoporella excellens* (YPM cat. no. 20473). YPM (Twenhofel 47); Cape Eagle; *Ptilodictya ensiformis* (YPM cat. no. 20820). YPM coll. no. 3063/58; lower zone, Cape Henry; *Ptilodictya ensiformis* (YPM cat. no. 20819); *Pachydictya* n. sp. YPM (Twenhofel 1227); unit 24, Vaural River section; *Ptilodictya ensiformis.* USNM cat. no. 69034, GSC 2248; Point Laframboise; *Stictoporella excellens.* YPM (Twenhofel 114); Point Laframboise; *Ptilodictya ensiformis.*

Becscie formation:
- Zone 1. YPM coll. no. 3063/62; west side of Fox Bay; *Ptilodictya sulcata; Pachydictya* n. sp. YPM coll. no. 3063/63; Reef Point; *Ptilodictya sulcata; Phaenopora superba.* USNM cat. no. 69044; Cape Eagle; *Stictoporella excellens.*
- Zone 4. USNM cat. no. 69051; West Becscie River cliff; *Ptilodictya sulcata.*

Gun River formation:
- Zone 3. USNM cat. no. 143050; Hannah Cliffs; *Ptilodictya canadensis.* USNM cat. nos. 143039 and 143049; Hannah Cliffs; *Ptilodictya sulcata; Ptilodictya canadensis.* YPM coll. no. 3063/98; east Gun River; *Ptilodictya sulcata.* YPM coll. no. 3063/104; St. Mary Cliff no. 3; *Ptilodictya sulcata; Phaenopora superba.*

Jupiter formation:
- Zone 1. YPM coll. no. 3063/111; Cape MacGillvray; *Ptilodictya sulcata.* YPM (Twenhofel 67), USNM cat. no. 69073; Cape Sand Top; *Ptilodictya sulcata; Stictoporella* sp. YPM (Twenhofel 1755); East Cliff; *Ptilodictya ensiformis.* YPM coll. no. 1391/1755; East Cliff; *Ptilodictya ensiformis.*
- Zone 2. YPM (Twenhofel 39); Cape Ottawa; *Ptilodictya ensiformis; Ptilodictya sulcata.*
- Zone 4. USNM cat. no. 69093; unit 8, east

Jupiter Cliff; *Stictoporella excellens*. YPM (Twenhofel 1249); east Jupiter Cliff, upper part; *Ptilodictya sulcata*. USNM cat. no. 143038: east Jupiter Cliff; *Stictoporella excellens*. YPM coll. no. 3063/118; east Jupiter Cliff; *Ptilodictya ensiformis*. YPM coll. no. 3063/75; East Cliff E; *Ptilodictya sulcata; Ptilodictya ensiformis*. YPM coll. no. 3063/76; East Cliff D; *Ptilodictya ensiformis* (YPM cat. no. 20821); *Ptilodictya sulcata*.

Zone 4. YPM coll. no. 3063/77; East Cliff C; *Ptilodictya ensiformis*. YPM coll. no. 3063/78; East Cliff B; *Ptilodictya ensiformis; Ptilodictya sulcata*. YPM (Twenhofel 7240); East Cliff; *Ptilodictya sulcata*. (YPM cat. no. 20475). YPM (Twenhofel 14); units 4–6, East Cliff; *Ptilodictya ensiformis*. YPM (Twenhofel 45), YPM (Twenhofel 717); East Cliff, units 4–5; *Ptilodictya ensiformis*. YPM (Twenhofel 109); East Cliff; *Ptilodictya ensiformis; Ptilodictya sulcata*. YPM coll. no. 3063/82; East Cliff G; *Ptilodictya sulcata*. YPM coll. no. 3063/84; East Cliff H; *Ptilodictya sulcata*.

Zone 5. GSC 15099; two miles east of Jupiter River; *Stictoporella excellens*.

Zone 7. YPM (Twenhofel 799); Southwest Point; *Ptilodictya ensiformis*.

Zone 8–9. USNM cat. no. 69049; Chaloupe Cliff (Shallop Cliff); *Ptilodictya canadensis*.

Zone 9. YPM coll. no. 3063/96; East Pavillon River Cliff; *Stictoporella excellens*. USNM cat. no. 69096; East Pavillon Cliff; *Ptilodictya sulcata*.

Zone 9. YPM coll. no. 3063/86; Bell River; *Stictoporella excellens* (YPM cat. no. 20474). USNM cat. no. 79533; Bell River; *Stictoporella excellens*. YPM (Twenhofel 23); east cliff of Iron River; *Ptilodictya sulcata*. YPM (Twenhofel 42); east cliff of Iron River; *Ptilodictya ensiformis; Ptilodictya sulcata*. YPM (Twenhofel 64); Iron River Cliffs; *Ptilodictya sulcata*. USNM cat. no. 69086; west Iron River cliff; *Ptilodictya sulcata*. YPM (Twenhofel 1399); cliffs near the mouth of Iron River; *Ptilodictya sulcata*. YPM (Twenhofel 1397); cliff west of Martin Brook; *Ptilodictya ensiformis*. USNM cat. no. 69106; west cliff of Martin Brook; *Ptilodictya sulcata*.

Zone 10. GSC 2501, USNM cat. no. 69084; The Jumpers; *Ptilodictya sulcata*. YPM (Twenhofel 41); lower beds, The Jumpers; *Ptilodictya sulcata*. YPM (Twenhofel 50); lower beds, The Jumpers; *Ptilodictya ensiformis; P. sulcata*. YPM (Twenhofel 721); lower beds, The Jumpers; *Stictoporella excellens* (YPM cat. no. 20818). USNM cat. no. 143040; mouth of Jupiter River; *Ptilodictya sulcata*. USNM cat. no. 69091; The Jumpers; *Stictoporella excellens*. YPM (Twenhofel 1519); lower beds, The Jumpers; *Stictoporella excellens* (YPM cat. no. 20470); *Ptilodictya sulcata*. USNM cat. no. 69104; west Pavillon River Cliff; *Ptilodictya sulcata*. YPM coll. no. 3063/92; one mile west of Box River; *Ptilodictya ensiformis; P. sulcata*. YPM coll. no. 3063/92a; east of Iron River Cliff; *Ptilodictya sulcata*.

Chicotte formation:

Zone 1. USNM cat. no. 11425; Chicotte Cliff; *Stictoporella excellens*. YPM coll. 3063/125; The Jumpers 2; *Pachydictya* n. sp. (YPM cat. no. 20812); *Ptilodictya sulcata*. YPM (Twenhofel 898); The Jumpers, upper beds; *Ptilodictya ensiformis*.

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SOME MISSISSIPPIAN FENESTRATE BRYOZOA FROM CENTRAL UTAH

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ABSTRACT—Fenestrate bryozoans from the Mississippian of central Utah are illustrated and described. Two families, the Fenestellidae and the Acanthocladiidae, are included in this study. The Fenestellidae studied include six genera, one subgenus, 23 species, 13 of which are new, and one new subspecies. The Acanthocladiidae include two genera and three new species.

The genus *Fenestella* includes six new species—*F. hamithensis*, *F. rarinodosella*, *F. tooelensis*, *F. acarinata*, *F. utahensis*, and *F. dissepinodaria*, one new subspecies, *F. serratula* subsp. *humbugensis*, and five previously described forms. *F. regallis* Ulrich, *F. parallela* Hall, *F. serratula* Ulrich, *F. rarinodosa* Condra & Elias and *F. tenax* Ulrich. The subgenus *Minilya* includes two new forms, *F.* (*Minilya*) *incipiens* and *F.* (*Minilya*) *crockfordae*. The genus *Archimedes* is represented by *A. macfarlani* Condra & Elias and *A. owenanus* Hall. *Fenestralia sancti-ludovici* Prout is present in the collection along with the new species *F. trifurcata*. *Hemitrypa* is represented by the new species *H. reticulata*. *Polypora* includes two new species, *P. micronodosa* and *P. stansburyensis*, and two previously described species, *P. cestriensis* Ulrich and *P. debilis* Elias. *Thamniscus* includes one new species, *T. raribifurcatus*. Among the Acanthocladiidae, the genus *Ptylopora* includes two new species, *P. condrai* and *P. eliasi*, and the genus *Septopora* is represented by one new species, *S. ulrichi*.

INTRODUCTION

A CONSIDERABLE amount of paleontological work has been done on the Mississippian faunas of central Utah. In the past, such studies have ignored or have given little attention to the bryozoan part of the fauna. This report is a study of the families Fenestellidae and Acanthocladiidae from central Utah.

The Mississippian System is represented in central Utah by five formations. They are from oldest to youngest: Madison group (Kinderhookian and lower Osagian), Deseret limestone (upper Osagian and lower Meramecian), Humbug formation (upper Meramecian), Great Blue limestone (lower Chesterian) and Manning Canyon shale (upper Chesterian and Lower Pennsylvanian).

The Madison group is composed of two as yet unnamed formations, a lower dolomite and an upper limestone. In the Tintic mining district the lower formation averages about 280 feet thick and contains eight distinctive units. The top unit, the "Curley limestone," is considered to be of algal origin (Proctor & Clark, 1956). Much of this member has been dolomitized. The upper formation of the Madison group is divided into two units. The lower unit is 375 feet thick and is composed of dark blue-gray fine to coarse-grained limestone. The upper unit is 125 feet thick and consists mainly of a fine-grained cherty limestone.

The Deseret limestone contains three members. The lower member, a black phosphatic shale with minor amounts of cherty limestone, ranges from 10 to 150 feet thick. The middle member is 450 feet thick in the Tintic district and is made up of blue-gray sandy to silty or cherty limestone. The upper member is a coquinoid limestone with some beds of fine-grained limestone and medium-grained sandstone.

The Humbug formation includes intercalated limestone, orthoquartzite sandstone, and dolomite. It is more than 2100 feet thick on Stansbury Island (Livingston, 1955) but thins rapidly to the east and south. There, the formation averages about 600 feet thick.

The Great Blue limestone conformably overlies the Humbug formation and includes four members. The basal member is about 400 feet thick and consists almost entirely of medium- to fine-grained limestone together with a few lenses of sandstone. The middle member consists of interbedded limestone and shale along with some orthoquartzite. It is about 150 feet thick. Above

the middle member is a thick shale and quartzite sequence averaging about 900 feet thick. The shale beds are fine-grained and fissile while the quartzite is fine to medium-grained. Typically, the shale is in the lower part of the member and the quartzite is in the upper part. The upper member of the Great Blue limestone is almost entirely limestone. It is about 600 feet thick and is fine- to medium-grained and thin-bedded.

The Manning Canyon shale overlies the Great Blue limestone. It is more than 1000 feet thick in central Utah and bridges the Mississippian-Pennsylvanian boundary. The lower (Mississippian) part is characterized by clay shales with some limestones (Moyle, 1958, Gilluly, 1932). There has been some question concerning the position of the Mississippian-Pennsylvanian boundary in the Manning Canyon shale. I do not wish to enter into this controversy here. R. W. Moyle (1958) presents the most recent discussion of this problem. My collections were taken from the lower part of the Manning Canyon shale up to and including a unit called the "Medial Limestone." My reasons for stopping at that point were that the "Medial Limestone" is a widespread and easily recognized unit close to the Mississippian-Pennsylvanian boundary and that there appeared to be more and better preserved bryozoans below it. There has been little work done previously on Mississippian bryozoans in central Utah although generic names have been included in several faunal lists from this area. Girty (*in* Calkins & Butler, 1943) noted *Fenestella* sp., *Fenestella* aff. *F. tenax* and *Stenopora* aff. *S. rudis* in American Fork Canyon near American Fork, Utah. Near Stockton, Utah, Girty (*in* Gilluly, 1932) included *Sulcoretepora*, *Polypora*, *Pinnatopora*, *Rhombopora* and *Stenopora* aff. *S. ramosa*. Elias (*in* Arnold, 1956) reports the following from the Great Blue limestone in the vicinity of Flux, Utah: *Fenestrellina* cf. *F. quadracimalis* McCoy, *Fenestella albida* Hall, *F. plebeia* McCoy, *F. fenestratum* Young & Young, *F. tenax* Ulrich, *Polypora striata* Cumings, *Hemitrypa nodosa* Ulrich, *Rhombopora* sp. and *Sulcoretepora* sp.

My collection includes the above genera and, in addition, others from areas that have not been previously sampled. A few genera of nonfenestrate bryozoans were also recovered but are not presented in this report. The reader should be reminded that this was a reconnaissance study. No doubt many Mississippian forms still remain to be described in central Utah.

The family Fenestellidae is represented by 12 species of *Fenestella*, two species of *Archimedes*, two species of *Fenestralia*, four species of *Polypora*, one species of *Hemitrypa*, one species of *Thamniscus*, and two species of *Minilya*. The family Acanthocladiidae is represented by two species of *Ptylopora* and one species of *Septopora*.

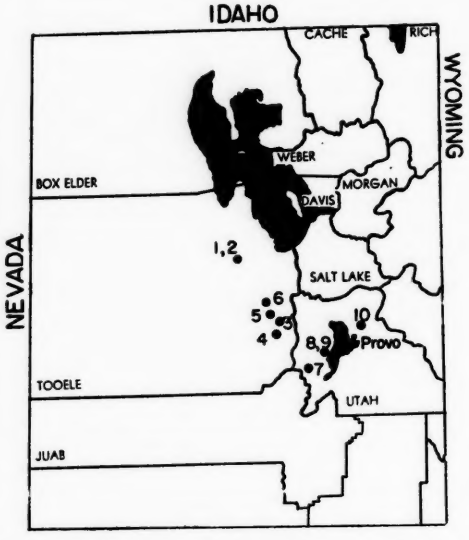
COLLECTING LOCALITIES

The complete Mississippian fauna was not collected at all localities. After each locality, it is indicated which part of the section was sampled.

1. Northern Stansbury Mountains. On north side of hill approximately one-half mile north of northernmost lime quarry 10 miles west of Grantsville, Utah in sec. 32, T. 1 S., R. 6 W., Timpie Quadrangle, Tooele County. Deseret limestone. BYU Locality 11030.

2. Same as 1. Humbug formation. BYU Locality 11031.

3. Soldier Canyon. About a half mile above



TEXT-FIG. *1*—Map of Mississippian collecting localities in central Utah.

its mouth, sec. 33, T. 5 S., R. 4 W. Stockton Quadrangle, Tooele County. Manning Canyon shale. BYU Locality 11011.

4. Sunshine Canyon. Immediately southeast of Old Sunshine Mine, in center of NE¼, sec. 29, T. 6 S., R. 3 W., Fairfield Quadrangle, Tooele County. Great Blue limestone. BYU Locality 11032.

5. Porphyry Hill. North of Mercur, Utah in NE¼, sec. 31, T. 5 S., R. 3 W., Fairfield Quadrangle, Tooele County. Long Trail member of Great Blue limestone. BYU Locality 11033.

6. Manning Canyon, about a half mile below the head in sec. 4, T. 6 S., R. 3 W., Fairfield Quadrangle, Utah County. Manning Canyon shale. BYU Locality 11024.

7. Rattlesnake Spur. Located in SE¼. sec. 1, T. 9 S., R. 3 W., approximately two miles west of Allens Tank on Allens Ranch. Allens Ranch Quadrangle. Deseret limestone. BYU Locality 11034.

8. Cedar Valley Hills. West side of Lake Mountain in NE¼, sec. 32, T. 7 S, R. 1 W., Utah County. Gardner group. BYU Locality 11035.

9. Same as 8. Humburg formation. BYU Locality 11036.

10. Provo Rock Canyon. Two miles east of Brigham Young University, Provo, Utah, in sec. 2, T. 6 S., R. 3. E., Humburg formation. BYU Locality 11037.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the advice of J. K. Rigby and H. J. Bissell. Also, gratitude is expressed to James Baer, R. W. Moyle, and Ronald Zeller who accompanied the author in the field and helped in making collections.

DISPOSITION OF COLLECTION

The collection is in the Types and Stratigraphic Collection Repositories, Brigham Young University, Provo, Utah.

SYSTEMATIC DESCRIPTIONS

Family FENESTELLIDAE King, 1850

Genus FENESTELLA Lonsdale, 1839

FENESTELLA REGALIS Ulrich

Pl. 133, figs. 5,6

Fenestella regalis ULRICH, 1888, Denison Univ. Sci. Labs, Bull., v. 4, pt. 1, p. 70–71; ULRICH, 1890, Illinois Geol. Survey, v. 8, p. 538–539, pl. 50, figs. 1,1a, pl. 54, fig. 5; KOENIG, 1957, Jour. Paleontology, v. 32, p. 134, pl. 22, figs. 2,6.

Description.—The zoarium is a fenestrate expansion of semirigid branches. The intervals at which bifurcations occur could not be determined but probably exceed 6 mm. There is no apparent bunching of the branches near the margins of the frond.

Branches are relatively strong. Average width below a bifurcation is 0.55 mm.; above, 0.34 mm. Variability of branch width below a bifurcation ranges from 0.40 mm. to 0.61 mm.; above, 0.26 mm. to 0.40 mm. Ratio of branch width to fenestrule width is 1 to 1 or 1.5. Variability of branches in 10 mm. is 9 to 13. Reverse of branches is moderately convex and smooth. Striations appear on the weathered surface. Obverse side is strongly convex, having a median keel bearing nodes.

The dissepiments are strong. Their width is about one-half that of branches, with an average width of 0.24 mm. Variability ranges from 0.20 mm. to 0.26 mm. The dissepiments are strongly arched and smooth on the reverse, depressed below the surface on the obverse side and flush with it on the reverse.

The fenestrules are elongate-oval to elongate-quadrate in outline, having an average length of 2.10 mm. Variability ranges from 1.40 mm. to 2.80 mm. Width ranges from 0.49 mm. to 0.60 mm. and averages 0.55 mm. Variability of fenestrules in 10 mm. is 3 to 5.

Zooecial apertures are large and circular in outline. Their average diameter is 0.18 mm. They are alternately arranged and spaced at intervals of about one diameter. The peristome is moderately well developed. Variability of zooecia in 5 mm. is 13 to 15.

Median nodes are present on the obverse face. Distance between nodes averages 0.65 mm. and ranges from 0.43 mm. to 0.80 mm. Variability of nodes in 5 mm. is 7 to 11.

Zoarial Formula.—9–13/3–5//13–15/7–11.

Discussion.—This form agrees closely with Ulrich's original types (1888) from the Keokuk limestone. In his description he notes 9 to 10 branches in 10 mm., 4 to 5 fenestrules in 10 mm., 14 zooecia in 5 mm. and the nodes on the carina spaced about 0.80 mm. apart. In the Utah form the nodes

are closer together, averaging only 0.65 mm. between. There is some difference in the width of the branches. Ulrich's form reaches a maximum of 0.90 mm., while the Utah form has a maximum of 0.61 mm.

Occurrence.—Deseret limestone, BYU Localities 11030 and 11034.

FENESTELLA PARALLELA Hall
Pl. 13, figs. 9,12

Fenestella parallela HALL, 1885, Ann. Rpt. State Geologist (N.Y.), pl. 1, fig. 7; HALL, 1886, Fifth Annual Rpt. State Geologist (N.Y.), pl. 44, figs. 8–18; HALL & SIMPSON, 1887, Paleontology of N.Y., v. 6, p. 107, pl. 44; KOENIG, 1957, Jour. Paleontology, v. 32, p. 138–140, pl. 21, fig. 3.

Description.—The zoarium is a fenestrate expansion of flexuous and semirigid branches. Bifurcations occur at intervals of about 4.5 mm. There is no apparent bunching of the branches.

The branches are moderately strong. The average width below a bifurcation is 0.63 mm.; above 0.28 mm. Variability of branch width below a bifurcation ranges from 0.60 mm. to 0.68 mm.; above, 0.25 mm. to 0.35 mm. The ratio of branch width to fenestrule width is about 1:1. Variability of branches in 10 mm. is 15 to 17. Reverse of branches is moderately convex and smooth. The obverse side is strongly arched, with median keel bearing nodes.

Dissepiments are slender. Their width is about one half that of branches, with an average width of 0.16 mm. Variability ranges from 0.12 mm. to 0.20 mm. Dissepiments are smooth and moderately arched on the reverse side, depressed below the surface on the obverse side and depressed or flush with it on the reverse.

The outline of the fenestrule is elongate-oval to elongate-quadrate, averaging 0.75 mm. in length. Variability ranges from 0.65 mm. to 0.86 mm. The width ranges from 0.29 mm. to 0.38 mm. and averages 0.33 mm. Variability of fenestrules in 10 mm. is 12 to 14.

The zooecial apertures are large and circular to oval in outline, having an average diameter of 0.13 mm. They are alternately arranged and spaced at intervals of one diameter or less. The peristome is poorly developed. Variability of zooecia in 5 mm. is 15 to 20.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.30 mm. to 0.68 mm. and averages 0.44 mm. Variability of nodes in 5 mm. is 14 to 16.

Zoarial Formula.—15–17/12–14//15–20/14–16.

Discussion.—This form agrees quite closely with Hall's original description. The main difference is that the Utah specimens have more apertures per 10 mm. and exhibit a less variable meshwork.

Occurrence.—Deseret limestone, BYU Locality 11034.

FENESTELLA SERRATULA Ulrich subsp. HUMBUGENSIS Burckle, n. subsp.
Pl. 131, figs. 3,7,10

Description.—The zoarium is a fenestrate expansion of flexuous and semirigid branches. Bifurcations occur at intervals of 0.70 mm. to 6.00 mm. They are more numerous and closer together in the initial stages of the frond. There is a noticeable bunching of the branches, near the margins. The frond is attached by one main stem and by several secondary stems from individual branches.

Branches are slender. Average width below a bifurcation is 0.34 mm.; above, 0.24 mm. Variability of branch width below a bifurcation ranges from 0.30 mm. to 0.39 mm.; above, 0.21 mm. to 0.27 mm. The ratio of branch width to fenestrule width is about 1:1 or 2:1. Variability of branches in 10 mm. is 21 to 28. Reverse of branches is gently convex and smooth. The obverse side is strongly convex, with median keel bearing row of regularly spaced conical nodes.

Dissepiments are slender. Their width is normally about half that of the branches, averaging 0.12 mm. Variability ranges from 0.09 mm. to 0.15 mm. Dissepiments are smooth on the reverse side, striated on the obverse, depressed just below the surface on the obverse and flush with it on the reverse.

Fenestrules are oval to elongate-quadrate. Their length ranges from 0.30 mm. to 0.60 mm. and averages 0.41 mm. Width averages 0.22 mm. and ranges from 0.15 mm. to 0.29 mm. Variability of fenestrules in 10 mm. is 18 to 24.

Zooecial apertures are small and circular, encroaching slightly upon the fenestrules,

with an average diameter of 0.07 mm. Apertures are arranged alternately and spaced at intervals of about 1 to 1.5 diameters. Normally they are disposed so that one or two apertures adjoin a fenestrule and one adjoins each dissepiment. The peristome is well developed. There are 20 to 26 apertures in 5 mm.

Median nodes are present on the obverse face. The distance between nodes averages 0.24 mm. and ranges from 0.19 mm. to 0.32 mm. Delicate stellate processes are developed on the apices of the nodes. Most of them have been removed by weathering, however. Variability of nodes in 5 mm. is 25 to 29.

Zoarial Formula.—21–28/18–24//20–26/25–29.

Discussion.—Condra & Elias (1944) and Elias & Condra (1957) referred to a variety of *Fenestella serratula* associated with *Archimedes moorei* Condra & Elias as having heavy "transverse, luniform bars" at the apices of the nodes. I can find no reference in which this subspecies has been named and so have named it from the Utah specimen, even though it was not found in association with any *Archimedes*.

According to some workers, this form should be placed in the genus *Cervella* (Chronic *in* Newell, Chronic, & Roberts, 1949) or in the subgenus *Cervella* (Elias & Condra, 1957). I subscribe to neither of these views. It seems unwise to make a generic or subgeneric designation upon a slight modification of the carinal nodes. A modification which, it seems, is not everywhere present and can be removed easily by weathering. For this reason, I propose that the term *Cervella* be discarded as a generic or subgeneric name.

Occurrence.—Lower Humbug formation, BYU Locality 11037.

Holotype.—Brigham Young University Specimen No. 5001.

FENESTELLA HAMITHENSIS Burckle, n. sp.
Pl. 131, fig. 13; Pl. 129, fig. 4

Description.—The zoarium is a fenestrate expansion of semirigid branches. Distance between bifurcations ranges from 1.5 mm. to 5.0 mm. The bifurcations are closer and more numerous in the initial portions of the frond. There is some bunching of the branches near the margins of the frond.

Branches are moderately strong. Their average width below a bifurcation is 0.51 mm.; above, 0.31 mm. Variability of branch width below a bifurcation ranges from 0.46 mm. to 0.65 mm.; above, 0.23 mm. to 0.48 mm. The ratio of branch width to fenestrule width is about 1 to .75. Variability of branches in 10 mm. is 16 to 20. The reverse of branches is moderately arched and smooth. No nodes are present. The obverse side is strongly arched, with median keel bearing nodes.

Dissepiments are moderately strong. Their width is normally about two-thirds that of branches, averaging 0.20 mm. Variability ranges from 0.17 mm. to 0.25 mm. Dissepiments are smooth and gently convex on the obverse side, smooth and strongly arched on the reverse, depressed or flush with the surface on the obverse side, flush with the surface on the reverse.

Fenestrules are elongate-oval, with an average length of 0.69 mm. Range is from 0.60 mm. to 0.80 mm. Width ranges from 0.22 mm. to 0.37 mm. and averages 0.27 mm. Variability of fenestrules in 10 mm. is 11 to 13.

Zooecial apertures are small and circular in outline, with an average diameter of 0.06 mm. They are arranged alternately and spaced at intervals of almost two diameters. Normally four apertures, sometimes three, adjoin each fenestrule. The peristome is moderately well developed. Variability of apertures in 5 mm. is 20 to 26.

Median nodes are present on the obverse face. Distance between nodes averages 0.79 mm. and ranges from 0.75 mm. to 0.90 mm. Nodes usually occur at junction of dissepiments and branches. Variability of nodes in 5 mm. is 8 to 9.

Zoarial Formula.—16–20/11–13//20–26/8–9.

Discussion.—This form suggests *F. rarinodosa* Condra & Elias in general outline. The principal difference is that it has fewer branches (16 to 20 versus 19 to 25 for *F. rarinodosa*) and fewer fenestrules (11 to 13 versus 13 to 19 for *F. rarinodosa*). *F. rarinodosa* also normally has three apertures to the fenestrule, while this form typically displays four.

Occurrence—Lower Humbug formation, BYU Locality 11036.

Holotype.—Brigham Young University Specimen No. 5003.

FENESTELLA RARINODOSA Condra & Elias
Pl. 131, figs. 1,5

Fenestella rarinodosa CONDRA & ELIAS, 1944, Geol. Soc. America, Spec. Paper 53, p. 77–78, pl. 13, figs. 9–12.

Description.—The zoarium is a fenestrate expansion of flexuous and semirigid branches. Bifurcations occur at intervals ranging from 2.4 mm. to 12.2 mm. They appear to be more numerous in the initial portion of the frond.

Branches are moderately strong. Their average width below a bifurcation is 0.52 mm. above, 0.28 mm. Variability of branch width below a bifurcation ranges from 0.47 mm. to 0.60 mm.; above, 0.20 mm. to 0.35 mm. The ratio of branch width to fenestrule width is about 1 to 1. In 10 mm. variability of branches is 20 to 25. The reverse side is gently convex and either striated or smooth. The obverse side is strongly arched, with median keel bearing nodes.

Dissepiments are strong. Their width is about one half that of the branches, the average being 0.23 mm. Variability ranges from 0.18 mm. to 0.27 mm. Dissepiments are smooth or pustulose on the reverse side, smooth and bearing carina on the obverse side. They are depressed slightly beneath the surface on the obverse side and flush with it on the reverse.

Fenestrules are oval to quadrate, sometimes circular, with an average length of 0.44 mm. The range is from 0.32 mm. to 0.55 mm. The width ranges from 0.15 mm. to 0.27 mm. and averages 0.21 mm. Variability of fenestrules in 10 mm. is 13 to 20.

Zooecial apertures are moderately large and circular to oval in outline, having an average diameter of 0.10 mm. Apertures are arranged alternately and spaced at intervals of one diameter or less. Normally, three apertures adjoin each fenestrule. The peristome is faint. Variability of apertures in 5 mm. is 22 to 26.

Elongate median nodes are present on a strong carina on the obverse face. Distance between nodes ranges from 0.58 mm. to 0.75 mm. and averages 0.65 mm. Usually they are placed near the juncture of the dissepiment and the branch. Variability of nodes in 5 mm. is 7 to 10.

Zoarial Formula.—20–25/13–20//22–26/7–10.

Discussion.—This form generally agrees with *F. rarindosa* Condra & Elias, although the meshwork formula is slightly more variable. Condra & Elias (1944) reported 20 to 23 branches, 15 to 17 fenestrules, 22 to 24 zooecia and 7 to 8 nodes.

Occurrence.—Lower Humbug formation, BYU Locality 11036.

FENESTELLA SERRATULA Ulrich
Pl. 131, figs. 4,6

Fenestella serratula ULRICH, 1890, Ill. Geol. Survey, v. 8, p. 544, pl. 50, figs. 5–5c; KEYES, 1894, Paleontology of Missouri, Missouri Geol. Survey, v. 5, p. 23; CUMINGS, 1906, Indiana Dept. Geology and Nat. Resources, 30th Annual Rpt., p. 1280, pl. 30, figs. 2–2c, 3, 3a; CONDRA & ELIAS, 1944, Geol. Soc. America, Spec. Paper 53, p. 72–76, pl. 13, figs. 6–8; pl. 21, figs. 4,5; pl. 36, fig. 3; KOENIG, 1957, Jour. Paleontology, v. 32, p. 137–138, pl. 21, fig. 5.

Description.—The zoarium is a fenestrate expansion of flexuous and semirigid branches. Bifurcations occur at intervals of 2.4 mm. to 9.5 mm. and quite possibly more. Bifurcations are less numerous and the branches more closely spaced near the margins of the frond.

Branches are moderately strong. The average width below a bifurcation is 0.46 mm.; above, 0.23 mm. Variability of branch width below a bifurcation ranges from 0.40 mm. to 0.55 mm.; above, 0.19 mm. to 0.30 mm. The ratio of branch width to fenestrule width is about 1 to .75 or .50. Variability of branches in 10 mm. is 22 to 28. Reverse of branches is gently convex and striated, obverse side more strongly convex with low median keel bearing regularly spaced nodes.

Dissepiments are moderately strong. Their width is about one half that of the branches, with an average of 0.18 mm. Variability ranges from 0.13 mm. to 0.22 mm. Dissepiments are smooth or pustulose on either side, depressed below the surface on the obverse side, flush with the surface or depressed slightly below it on the reverse.

Fenestrules are oval to elongate-oval in outline. Their length ranges from 0.37 mm. to 0.50 mm. and averages 0.44 mm. Their width averages 0.17 mm. and ranges from

0.13 mm. to 0.23 mm. Variability of fenestrules in 10 mm. is 17 to 23.

Zooecial apertures are small and circular, with an average diameter of 0.06 mm. They are alternately arranged and spaced at intervals of one diameter or more. Usually they are disposed so that two apertures adjoin a fenestrule and one adjoins each dissepiment. The peristome is well developed but usually removed by weathering. Variability of apertures in 5 mm. is 24 to 28.

Median nodes are present on the obverse face. The distance between nodes averages 0.26 mm. and ranges from 0.20 mm. to 0.30 mm. Variability in 5 mm. is 25 to 28.

Zoarial Formula.—22–28/17–23//24–28/25–28.

Discussion.—I have found this form in only one locality. Its meshwork formula agrees quite closely with that given by Condra & Elias (1944) for Warsaw specimens of *F. serratula*. They report a variability of 22 to 30 branches, 17 to 24 fenestrules, 25 to 28 zooecia and 20 to 28 nodes. Chester members of this species, according to the same authors, have 20 to 27 branches, 18 to 24 fenestrules, 22 to 26 zooecia and 15 to 25 nodes. A comparison of the two formulas suggests that the Utah form is slightly more advanced than the Warsaw forms.

Occurrence.—Lower Humbug formation, BYU Locality 11036.

FENESTELLA TOOELENSIS Burckle, n. sp.
Pl. 131, figs. 8,11

Description.—The zoarium is a fenestrate, flexuous expansion. The largest specimen in the collection measures 9 mm. long and 18 mm. wide. Branches fan out in smooth curves from the axial portion and bifurcate at intervals of 1.9 mm. to 3.5 mm. Branches in the margins of the frond tend to be more crowded.

Branches are moderately strong. Their average width below a bifurcation is 0.50 mm.; above, 0.28 mm. Total variability of branch width below a bifurcation ranges from 0.41 mm. to 0.57 mm.; above, 0.25 mm. to 0.31 mm. The ratio of branch width to fenestrule width is about 1.5 to 1. In 10 mm. the variability of branches is 23 to 27. Reverse of branches is angular and striated to smooth, normally without nodes but sometimes bearing them at juncture of branch and fenestrule. Variability of reverse-side nodes in 5 mm. is 8 to 10. Obverse of branches is convex and bears medial, more or less regularly spaced, elongated nodes.

Dissepiments are strong. The width is normally about one half that of branches, with an average width of 0.19 mm. Total variability of width ranges from 0.17 mm. to 0.30 mm. Dissepiments on both sides are smooth, depressed below the surface on the obverse side and slightly raised or flush with the surface on the reverse.

Fenestrules are oval to elongate-quadrate. The average length is 0.44 mm. Variability ranges from 0.35 mm. to 0.50 mm. The width averages 0.18 mm. and ranges from 0.14 mm. to 0.21 mm. Variability of fenestrules in 10 mm. is 16 to 24.

Zooecial apertures are roughly circular in outline. Their average diameter is 0.09 mm. They are alternately arranged and spaced at intervals of one diameter or slightly less. Usually they are disposed so that one adjoins a fenestrule and one adjoins each dissepiment. The peristome is well developed. Variability of apertures in 5 mm. is 20 to 24.

Median nodes are well developed on obverse face. The average distance between nodes is 0.30 mm. with a range from 0.25 mm. to 0.45 mm. Variability of nodes in 5 mm. is 16 to 20.

Zoarial Formula.—23–27/16–24//20–24/16–20.

Discussion.—This form suggests *F. rectangularis* Condra & Elias, differing mainly in the number of nodes per 5 mm. (14 to 17). Other measurements of *F. rectangularis* include 20 to 26 branches, 17.5 to 24 fenestrules and 23 to 25 apertures. *F. tooelensis* n. sp. is also close to the range of *F. serratula* Ulrich. This may be a transitional form between *F. rectangularis* and *F. serratula*.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5004.

FENESTELLA ACARINATA Burckle, n. sp.
Pl. 133, figs. 7,8

Description.—The zoarium is a flexuous expansion of irregularly arranged coarse branches. Bifurcations occur at intervals of 1.8 mm. to 3.2 mm. and are more numerous

in the initial portion of the frond. There is no apparent bunching of the branches near the margins.

Branches are robust. The average branch width below a bifurcation is 0.91 mm.; above, 0.38 mm. Variability of branch width below a bifurcation has a range of 0.80 mm. to 0.96 mm.; above, 0.32 mm. to 0.51 mm. The ratio of branch width to fenestrule width is about 1 or 1.5 to 1. Variability of branches in 10 mm. is 12 to 16. Reverse of branches is gently convex and striated. Obverse side is broadly arched, bearing medial, conical nodes.

Dissepiments are strong. Their width is normally about one half that of branches and averages 0.30 mm. Variability ranges from 0.22 mm. to 0.42 mm. Dissepiments on either side are essentially smooth. They are depressed and somewhat convex on the obverse side, while on the reverse they appear sharp, almost keeled, and flush with the surface or raised slightly above it.

Fenestrules are oval to elongate-quadrate. Their length ranges from 0.40 mm. to 1.00 mm. and averages 0.75 mm. The width averages 0.28 mm. and ranges from 0.17 mm. to 0.48 mm. Variability of fenestrules in 10 mm. is 12 to 16.

Zooecial apertures are large and circular, having an average diameter of 0.13 mm. The apertures are arranged alternately and spaced at intervals of slightly less than one diameter. The peristome is well developed. Variability of apertures in 5 mm. is 16 to 20.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.69 mm. to 1.00 mm. and averages 0.81 mm. Variability in 5 mm. is 8 to 10.

Zoarial Formula.—12–16/12–16//16–20/8–10.

Discussion.—In general outward appearance this form is similar to *F. megalopora* Deiss. It differs in having thicker branches, a coarser zoarial formula and in lacking a carina.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5005.

FENESTELLA TENAX Ulrich
Pl. 131, fig. 2

Fenestella tenax ULRICH, 1888, Denison Univ. Sci. Labs. Bull. 4 p. 71; ULRICH, 1890, Ill. Geol. Survey, v. 8, p. 546, pl. 51, fig. 5 2–2c; CUMINGS, 1906, Indiana Dept. Geol. and Nat. Resources, 30th Ann. Rpt., p. 1279, pl. 30, fig. 1, pl. 21, figs. 1–16; CONDRA & ELIAS, 1944, Geol. Soc. America, Spec. Paper 53 p. 99–102, pl. 21, figs. 1–3; ELIAS & CONDRA, 1957, Geol. Soc. America Mem. 70, p. 106–107, pl. 10, figs. 1,2.

Fenestella submicroporata SHULGA-NESTERENKO,

EXPLANATION OF PLATE 129

FIG. *1*—*Fenestella* sp. A view of the obverse side showing the poor state of preservation to be found in many Madison and Deseret forms in my collection. ×5.

2,3—*Septopora ulrichi* Burckle, n. sp. *2*. View showing arrangement of the zooecia. ×15. *3*. View showing obverse side of zoarium. ×5. BYU Holotype No. 5017.

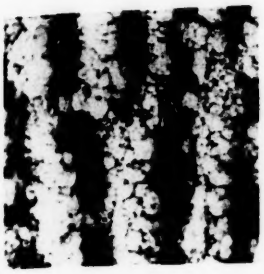
4—*Fenestella hamithensis* Burckle, n. sp. View showing obverse side of frond. ×5. BYU Holotype No. 5002.

5,9—*Fenestella* (*Minilya*) *crockfordae* Burckle, n. sp. *5*. View of obverse side of frond. ×5. *9*. Close-up of obverse side showing disposition of nodes. ×15. BYU Holotype No. 5009.

6,12—*Fenestralia sancti-ludovici* Prout. *6*. Close-up of obverse side showing arrangement of zooecia. ×15. *9*, View of obverse side of zoarium. ×5.

7,10—*Fenestralia trifurcata* Burckle, n. sp. *7*. View showing details of obverse side of frond. ×5. *10*. Close-up of obverse side of frond. ×15. BYU Holotype No. 5010.

8,11—*Fenestella* (*Minilya*) *incipiens* Burckle, n. sp. *8*. Close-up of frond showing disposition of nodes. ×15. *11*. View of obverse side of frond. ×5. BYU Holotype No. 5008.



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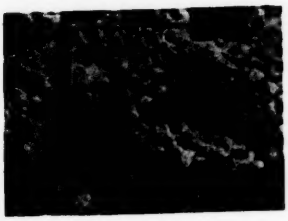

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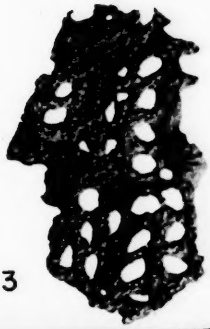

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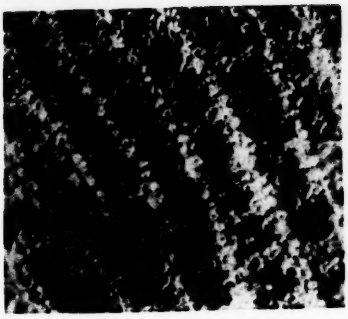

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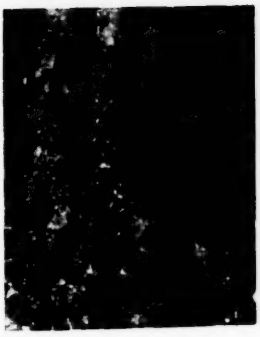

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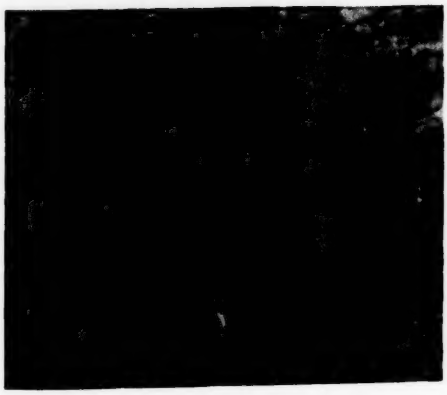

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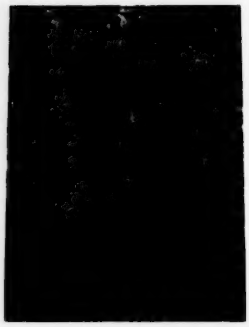

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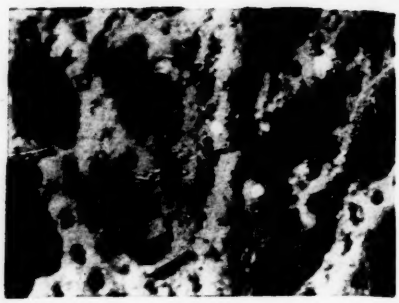

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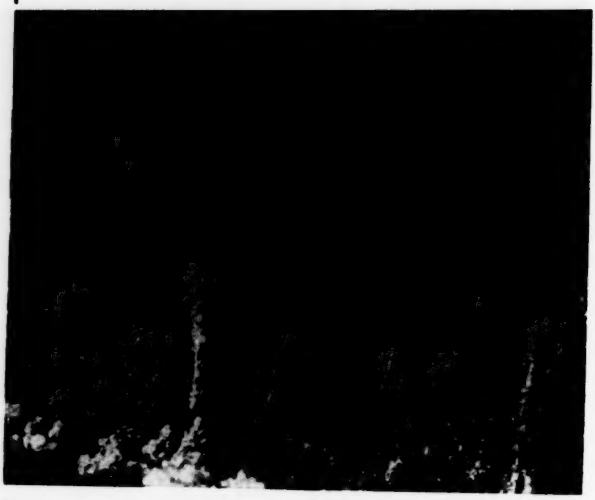

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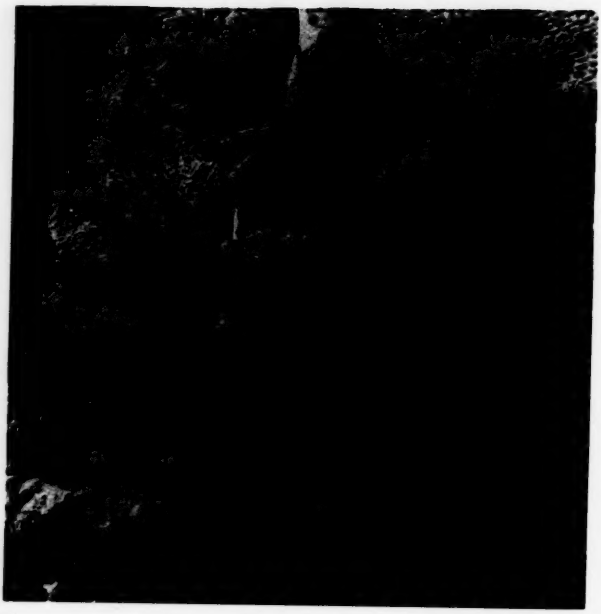

6

7

1952, Akad. Nauk S.S.S.R., Paleont. Inst. Trans., t. 37, p. 35–36, fig. 15, pl. 4, fig. 2.

Description.—The zoarium is a fenestrate, flexuous expansion. Bifurcations occur at intervals of 1.9 mm. to 6.2 mm. They are more numerous and the branches more spread out in the initial stages of the frond.

Branches are moderately strong. Their average width below a bifurcation varies from 0.45 mm. to 0.50 mm.; above, 0.20 mm. to 0.34 mm. The ratio of branch width to fenestrule width is about 1 to .5. Variability of branches in 10 mm. is 24 to 29. Reverse of branches is gently convex and striated. The obverse side is more strongly convex with low median keel bearing closely spaced nodes.

Dissepiments are slender. Their width is less than one half that of branches, with an average width of 0.12 mm. Variability ranges from 0.10 mm. to 0.15 mm. Dissepiments are striated on both sides and depressed slightly below the surface, also on both sides.

Fenestrules are oval to elongate-oval. Their length ranges from 0.30 mm. to 0.60 mm. and averages 0.41 mm. The width averages 0.18 mm. and ranges from 0.14 mm. to 0.20 mm. Variability of fenestrules in 10 mm. is 24 to 28.

Zooecial apertures are small and circular in outline. Their average diameter is 0.06 mm. They are alternately arranged and spaced at intervals of about one diameter. Usually they are disposed so that one adjoins a fenestrule and one adjoins each dissepiment. The peristome is well developed. Apertures in 5 mm. vary from 24 to 30.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.20 mm. to 0.27 mm. Variability of nodes in 5 mm. is 27 to 30.

Zoarial Formula.—24–29/24–28//24–30/27–30.

Discussion.—This form agrees quite closely with Ulrich's original description for Chesterian samples of this species except that the Utah form has a more variable meshwork. The fenestrule count (24 to 29) is more in agreement with Ulrich's Warsaw forms (28 to 29) than his Chester forms (23). Condra & Elias (1944) have already pointed out that, contrary to Ulrich's findings, the fenestrule count is higher in the Chester examples of *F. tenax* than in those from the Warsaw. The Utah forms tend to support the views of Condra & Elias.

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

FENESTELLA UTAHENSIS Burckle, n. sp.
Pl. 133, figs. 1,2

Description.—The zoarium is a fenestrate expansion of semirigid branches. Bifurcations occur at intervals of 2.6 mm. to 9.5 mm. There is no apparent bunching of the branches.

Branches are strong. Their average width below a bifurcation is 0.63 mm.; above, 0.40 mm. Variability of branch width below a bifurcation ranges from 0.54 mm. to 0.69 mm.; above, 0.34 mm. to 0.50 mm. The ratio of branch width to fenestrule width is about 1 to 1 or 1.5. Variability of branches in 10 mm. is 14 to 20. Reverse of branches is moderately convex and striated. The ob-

EXPLANATION OF PLATE 130

FIG. *1,2—Polypo[illegible] micronodosa* Burckle, n. sp. *1.* Close-up of obverse side. ×15. *2.* View of obverse side of frond. ×5. BYU Holotype No. 5012.

3,5—Ptylopora eliasi Burckle, n. sp. *3.* Close-up of main branch and several secondaries, ×15. *5.* View showing details of obverse side of frond. ×5. BYU Holotype No. 5016.

4,6—Archimedes macfarlani Condra & Elias. *4.* Close-up of rods connecting two fronds. ×15. *6.* View showing details of shaft. ×2.

7—Archimedes owenanus Hall. View showing details of shaft. ×2.

verse side has a strong median keel with regularly spaced, elongated nodes.

Dissepiments are relatively slender. Their width is about one-third to one-half that of the branches, averaging 0.17 mm. Variability ranges from 0.09 mm. to 0.20 mm. Dissepiments are striated on either side and depressed slightly below the surface on both sides.

Fenestrules are oval to elongate-oval. Their length ranges from 0.70 mm. to 1.00 mm. and averages 0.83 mm. The width averages 0.38 mm. and ranges from 0.30 mm. to 0.50 mm. Variability of fenestrules in 10 mm. is 10 to 13.

Zooecial apertures are moderately large and circular, having an average diameter of 0.10 mm. Apertures are alternately arranged and spaced at intervals of slightly less than one diameter. Normally, they are disposed so that one aperture adjoins each dissepiment. The peristome is moderately well developed. The number of apertures in 5 mm. is 20 to 22.

Median nodes are present on a strong carina on the obverse face. The distance between nodes ranges from 0.50 mm. to 0.95 mm. and averages 0.77 mm. Variability of nodes in 5 mm. is 7 to 12.

Zoarial Formula.—14–20/10–13//20–22/7–12.

Discussion.—This form differs from others in its coarse meshwork and small nodal count.

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

Holotype.—Brigham Young University Specimen No. 5006.

FENESTELLA DISSEPINODARIA Burckle, n. sp.
Pl. 133, figs. 9,10

Description.—The zoarium is a fenestrate expansion of semirigid branches. Bifurcations occur at intervals of 1.6 mm. to 8.0 mm. No bunching of the branches is apparent in the margins of the frond.

Branches are strong. Their average width below a bifurcation is 0.57 mm.; above, 0.34 mm. Variability of branch width below a bifurcation ranges from 0.51 mm. to 0.60 mm.; above, 0.30 mm. to 0.40 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 16 to 20. Reverse of branches is gently convex and granulo-striated. The obverse side is more strongly convex, with low median keel bearing regularly spaced nodes.

Dissepiments are moderately strong. Their width is normally about one-half that of branches and averages 0.19 mm. Variability ranges from 0.15 mm. to 0.25 mm. Dissepiments are smooth or pustulose on the reverse side, striated on the obverse side. One to two nodes are usually present on the obverse side of the dissepiments, which are flush with the surface on both sides. Occasional nodes occur at junction of branch and dissepiment on the reverse face.

Fenestrules are oval to elongate-quadrate. Their average length is 0.52 mm. The range is from 0.49 mm. to 0.60 mm. The width ranges from 0.22 mm. to 0.27 mm. and averages 0.25 mm. Variability of fenestrules in 10 mm. is 14 to 16.

Zooecial apertures are small and circular, having an average diameter of 0.08 mm. They are alternately arranged and spaced at intervals of slightly more than one diameter. The peristome is well developed and encroaching slightly upon the fenestrules. Variability of apertures in 5 mm. is 24 to 26.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.15 mm. to 0.25 mm. and averages 0.19 mm. Variability of nodes in 5 mm. is 27 to 35.

Zoarial Formula.—16–20/14–16//24–26/27–35.

Discussion.—Condra & Elias (1944) reported the presence of nodes on the dissepiments on the frond of *Archimedes macfarlani* Condra & Elias. The meshwork of this frond is slightly finer than the Utah form. They report 21–27/16.5–21//21–25/27–32.

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

Holotype.—Brigham Young University Specimen No. 5007.

FENESTELLA sp.
Pl. 129, fig. 1

Description.—The zoarium is a fenestrate expansion of flexuous branches. Bifurcations occur at intervals of 1.20 mm. to 4.70 mm. They appear to be more numerous in the axial portion of the frond. There is some bunching of the branches near the margins.

Branches are moderately strong. Their average width below a bifurcation is 0.58 mm.; above, 0.39 mm. Variability of branch width below a bifurcation ranges from 0.45 mm. to 0.75 mm.; above, 0.25 mm. to 0.52 mm. The ratio of branch width to fenestrule width is about 1 to 1 or 1.5. Variability of branches in 10 mm. is 8 to 16. Reverse of branches is strongly arched and pustulose. The obverse side is strongly convex, with median keel bearing nodes.

Dissepiments are slender. Their width is about one half that of the branches, with an average width of 0.24 mm. Variability ranges from 0.20 mm. to 0.30 mm. Dissepiments are strongly arched and pustulose on the reverse side, striated on the weathered surface. They are strongly convex and pustulose on the obverse side. Normally, the dissepiments are flush with the surface on the reverse side and depressed below it on the obverse.

The fenestrule outline is elongate-oval to elongate-quadrate. The length ranges from 0.76 mm. to 1.60 mm. and averages 1.09 mm. The width averages 0.45 mm. and ranges from 0.28 mm. to 0.58 mm. Variability of fenestrules in 10 mm. is 5 to 10.

Zooecial apertures are large and circular in outline, having an average diameter of 0.12 mm. Apertures are arranged alternately and spaced at intervals of one diameter or less. The peristome is absent. Variability of apertures in 5 mm. is 14 to 16.

Median nodes are present on the obverse face. The distance between nodes averages 0.54 mm. and ranges from 0.50 mm. to 0.90 mm. Variability of nodes in 5 mm. is 8 to 10.

Discussion.—The zoarial formula is not given here because the specimen has been considerably altered by silicification. This has served to obscure many of the features and for that reason I withhold any specific designation.

Occurrence.—Middle Deseret limestone, BYU Locality No. 11034.

FENESTELLA spp.

Discussion.—Many fenestellid bryozoans were observed in the Madison group. However, most of them were too fragmental to permit specific identification. In general outward appearance they are most like the coarser representatives from the overlying Deseret limestone. Most likely these two units have many species in common.

FENESTELLA (MINILYA) INCIPIENS Burckle, n. sp.
Pl. 129, figs. 8,11

Description.—The zoarium is a fenestrate expansion of semirigid branches. The species is represented by a single fragment and much of the character of the frond could not be determined. Bifurcations occur at intervals of 1.8 mm. to in excess of 5.0 mm.

Branches are moderately strong. Their average width below a bifurcation is 0.48 mm.; above, 0.31 mm. Variability of branch width below a bifurcation is 0.42 mm. to 0.51 mm.; above, 0.22 mm. to 0.34 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 20 to 24. Reverse of branches is moderately convex and smooth. The obverse side is more strongly convex and bears a closely spaced, slightly zigzag row of nodes.

Dissepiments are slender. Their width is about one-half to one-third that of the branches. The average width is 0.13 mm. Variability ranges from 0.12 mm. to 0.15 mm. Dissepiments are smooth or pustulose on either side, and depressed below the surface on both sides.

Fenestrules are quadrate to elongate-quadrate. The length ranges from 0.27 mm. to 0.35 mm. and averages 0.31 mm. The width averages 0.22 mm. and ranges from 0.19 mm. to 0.28 mm. Variability of fenestrules in 10 mm. is 23 to 24.

Zooecial apertures are small and circular. Their average diameter is 0.06 mm. Apertures are arranged alternately and spaced at intervals of about one diameter. They are disposed so that one aperture adjoins a fenestrule and one adjoins each dissepiment. The peristome is well developed. Apertures in 5 mm. number 20 to 24.

Median nodes are present on the obverse face. They are disposed in a zigzag fashion and each one adjoins an aperture. The zigzag nature of the nodes is not readily apparent except under high power. Variability of nodes in 5 mm. is 40 to 48.

Zoarial Formula.—20–24/23–24//20–24/40–48.

Discussion.—This marks the lowest occurrence of the subgenus *Minilya* in my ma-

terial. It is similar to *F.* (*Minilya*) *crockfordae* Burckle, n. sp. from the overlying Humbug formation of Utah except that its meshwork formula is somewhat finer.

Occurrence.—Deseret limestone, BYU Locality 11034.

Holotype.—Brigham Young University Specimen No. 5008.

FENESTELLA (MINILYA) CROCKFORDAE
Burckle, n. sp.
Pl. 129, figs. 5,9

Description.—The zoarium is a fenestrate expansion of flexuous and semirigid branches. Bifurcations occur at intervals of 1.6 mm. to 3.8 mm. and are more numerous in the initial stages of the frond. There is some bunching of the branches near the margins.

Branches are moderately strong. Their average width below a bifurcation is 0.52 mm.; above, 0.29 mm. Variability of branch width below a bifurcation ranges from 0.45 mm. to 0.57 mm.; above, 0.22 mm. to 0.34 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 20 to 24. Reverse of branches is moderately convex and smooth. Obverse of branches is strongly convex and bears a row of medial nodes disposed in a zigzag manner, each one adjoining a complimentary aperture.

Dissepiments are moderately strong. Their width is normally equal to or slightly less than that of the branches with an average of 0.22 mm. Variability ranges from 0.19 mm. to 0.24 mm. Dissepiments are smooth on both sides, depressed below the surface on the obverse side and flush with it on the reverse.

Fenestrules are quadrate to elongate-quadrate. The average length is 0.35 mm. Variability ranges from 0.23 mm. to 0.42 mm. The width ranges from 0.15 mm. to 0.32 mm. and averages 0.21 mm. Variability of fenestrules in 10 mm. is 18 to 20.

Zooecial apertures are circular in outline. Their average diameter is 0.09 mm. They are alternately arranged and spaced at intervals of about one diameter. Typically, one aperture adjoins a fenestrule and one adjoins each dissepiment. The peristome is moderately well developed. Variability of zooecia in 5 mm. is 19 to 21.

Median nodes are present on the obverse face. Nodes adjoin and are disposed in a zigzag manner. Variability of nodes in 5 mm. is 38 to 42.

Zoarial Formula.—20–24/18–20//19–21/38–42.

Discussion.—This form is most like *F. plummerae* Moore. It differs in having slightly fewer fenestrules per 10 mm. and fewer apertures per 5 mm. than *F. plummerae.*

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5009.

Genus ARCHIMEDES Owen 1838
ARCHIMEDES MACFARLANI
Condra & Elias
Pl. 130, figs. 4,6

Archimedes proutanus ULRICH, 1890, Illinois Geol. Survey, v. 8, p. 576–577, pl. 63, figs. 2,2b.

Archimedes macfarlani CONDRA & ELIAS, 1944, Geol. Soc. America, Spec. Paper 53, p. 150–152, pl. 8, figs. 3,4; pl. 31, figs. 2b, 3,4; pl. 32, fig. 1.

Description.—This species is represented by several specimens. Shaft diameter averages 1.5 mm. and ranges from 1.2 mm. to 1.8 mm. Volution height ranges from 3.5 mm. to 5.0 mm. and averages 4.2 mm., while flange averages 3.3 mm. and ranges from 2.5 mm. to 4.0 mm. The angle at which the frond leaves the screw varies from 55 to 65 degrees.

The frond is a fenestrate expansion of semirigid and flexuous branches. Bifurcations occur infrequently. There is no apparent bunching of the branches anywhere on the frond.

Branches are moderately strong. The average width below a bifurcation is 0.58 mm.; above, 0.34 mm. Variability of branch width below a bifurcation ranges from 0.55 mm. to 0.60 mm.; above, 0.30 mm. to 0.40 mm. The ratio of branch width to fenestrule width is about 1 to .75. Variability of branches in 10 mm. is 20 to 24. Reverse of branches is convex, striated and pustulose. Nodes may occur at the juncture of the branch and dissepiment and extend down into the frond below. The obverse side is convex, with a low carina bearing medial nodes.

Dissepiments are strong and slightly narrower than the branches. The average width is 0.32 mm. Variability ranges from 0.29 mm. to 0.41 mm. They are pustulose and flush with the surface on the reverse side, and pustulose and depressed slightly below the surface on the obverse.

Fenestrules are quadrate to elongate-quadrate. Their length ranges from 0.30 mm. to 0.50 mm. and averages 0.42 mm. The width averages 0.19 mm. and ranges from 0.15 mm. to 0.25 mm. Variability of fenestrules in 10 mm. is 16 to 20.

Zooecial apertures are small and circular in outline. Their average diameter is 0.09 mm. Zooecia are arranged alternately and spaced at intervals of one diameter, or slightly farther apart. The peristome is moderately well developed. Variability of zooecia in 5 mm. is 25 to 27.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.20 mm. to 0.31 mm. and averages 0.26 mm. Variability of nodes in 5 mm. is 25 to 26.

Zoarial Formula.—20–24/16–20//25–27/25–26.

Discussion.—The character of the screw differs somewhat from that described by Condra & Elias (1944). The screw diameter is not as variable and the volution height is slightly greater. The meshwork formula is much the same except that the Utah form has slightly more apertures per 5 mm. Condra & Elias (1944) reported the presence of nodes on the dissepiments on their specimens. These do not appear on the Utah forms. However, I feel that this does not warrant giving this form a separate specific designation.

Occurrence.—Upper Great Blue limestone and lower Manning Canyon shale, BYU Locality 11024. Collected by R. W. Moyle.

ARCHIMEDES OWENANUS Hall
Pl. 130, fig. 7

Fenestella (*Archimedes*) *owenana* HALL, 1857, Amer. Assoc. Adv. Sci., Pr., p. 178.
Archimedes owenanus ULRICH, 1890, Ill. Geol. Survey, v. 8, p. 568, 570–571, pl. 63, figs. 6–6c; KEYES, 1894, Paleontology of Missouri, Missouri Geol. Survey, v. 5, p. 26, pl. 33, fig. 2; CONDRA & ELIAS, 1944, Geol. Soc. America, Spec. Paper 53, p. 92–95, pl. 14, figs. 7–15.

Description.—This species is represented by a single specimen from the uppermost Chesterian of central Utah. Shaft diameter ranges from 1.6 mm. to 1.9 mm. and averages 1.7 mm. Flange diameter remains fairly constant around 5.5 mm. and the volution height ranges from 7.0 mm. to 7.5 mm. The angle at which the frond leaves the screw varies from 65 to 70 degrees.

The zoarium is a fenestrate expansion of semirigid branches. The complete zoarium was not observed but apparently bifurcations occur quite frequently.

Branches are moderately slender. The average width below a bifurcation is 0.55 mm.; above, 0.28 mm. Variability of branch width below a bifurcation ranges from 0.45 mm. to 0.70 mm.; above, 0.24 mm. to 0.40 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 19 to 21. Reverse of branches is gently arched and smooth or striated. The obverse side is strongly convex, with a carina bearing regularly spaced, low median nodes.

Dissepiments are slender. Their width is about one-half that of the branches, averaging 0.19 mm. Variability ranges from 0.15 mm. to 0.22 mm. Dissepiments are striated on the obverse, smooth on the reverse. They are gently convex and depressed below the surface on the obverse side and flush with it on the reverse.

Fenestrules are elongate-quadrate in outline. Their length ranges from 0.41 mm. to 0.60 mm. and averages 0.50 mm. The width averages 0.26 mm. and ranges from 0.20 mm. to 0.30 mm. Variability of fenestrules in 10 mm. is 16 to 17.

Zooecial apertures are small and circular in outline, having an average diameter of 0.09 mm. They are arranged alternately and spaced at intervals of one diameter or less. The peristome is moderately well developed. Variability of zooecia in 5 mm. is 20 to 22.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.31 mm. to 0.37 mm. and averages 0.33 mm. Variability of nodes in 5 mm. is 15 to 17.

Zoarial Formula.—19–21/16–17//20–22/15–17.

Discussion.—Only one representative of this species has thus far been found in central Utah and it agrees quite closely with the

description given by Condra & Elias (1944). The main difference is that the Utah form seems to be less variable in the measurement of screw and meshwork.

Occurrence.—Lower Manning Canyon shale, BYU Locality 11019. Collected by R. W. Moyle.

Genus FENESTRALIA Prout 1858

FENESTRALIA TRIFURCATA Burckle, n. sp.

Pl. 129, figs. 7,10

Description.—The zoarium is a fenestrate expansion of semirigid and flexuous branches. Bifurcations occur at undetermined intervals although they most probably are more than 2.5 mm. apart. The zoarium has been observed to trifurcate.

Branches are moderately strong. Their average width below a bifurcation is 0.69 mm.; above, 0.49 mm. Variability of branch width below a bifurcation ranges from 0.50 mm. to 0.85 mm.; above, 0.35 mm. to 0.65 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 17 to 19. Reverse of branches is strongly convex and smooth. The obverse side is strongly convex, with a median ridge bearing more or less regularly spaced nodes.

Dissepiments are moderately strong. Their width is normally about one half that of the branches. Variability ranges from 0.26 mm. to 0.52 mm. and averages 0.36 mm. Dissepiments are smooth on either side, being broadly arched on the obverse side, strongly convex on the reverse. Normally they are depressed just below the surface on the obverse side and flush with it on the reverse.

Fenestrules are oval to rectangular in outline. The length ranges from 0.87 mm. to 1.12 mm. and averages 1.01 mm. The width averages 0.43 mm. and ranges from 0.29 mm. to 0.60 mm. Variability of fenestrules in 10 mm. is 6 to 8.

Zooecial apertures are small and circular in outline. There are two rows of zooecia on each side of the median keel, 4 rows in all on each branch. The average diameter is 0.07 mm. Apertures are arranged alternately and spaced at intervals of about two diameters. The peristome is moderately developed. Variability of apertures in 5 mm. is 20 to 25.

Median nodes are present on the obverse face. The distance between nodes averages 0.81 mm. and ranges from 0.72 mm. to 1.00 mm. Variability of nodes in 5 mm. is 6 to 8.

Zoarial Formula.—17–19/6–8//20–25/6–8.

Discussion.—This form differs from *Fenestralia sancti-ludovici* Prout in having a less robust frond, more branches per 10 mm. and more apertures per 5 mm. *Fenestralia trifurcata* n. sp. has 17 to 19 branches, 6 to 8 fenestrules, 20 to 25 apertures and 6 to 8 nodes while *F. sancti-ludovici* Prout has 9.5 to 11.5 branches, about 6 fenestrules, 18 apertures and about 5 to 6 nodes.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5010.

FENESTRALIA SANCTI-LUDOVICI Prout

Pl. 129, figs. 6,12

Fenestralia sancti-ludovici PROUT, 1858, Acad. Sci. St. Louis, Trans, 1, p. 234, pl. 15, figs. 1,1a; ULRICH, 1890, p. 604, pl. 5; KEYES, 1894, p. 30; SIMPSON, 1895, p. 717, fig. 62; SIMPSON, 1897, p. 503, figs. 42,43.

Description.—The zoarium is a fenestrate expansion of flexuous branches. Bifurcations occur at intervals of 1.5 mm. to 8.0 mm. They are more numerous in the initial stages of the frond. There is a slight bunching of the branches near the margins.

Branches are strong. The average width below a bifurcation is 0.70 mm.; above, 0.46 mm. Variability of branch width below a bifurcation ranges from 0.65 mm. to 0.82 mm.; above, 0.35 mm. to 0.60 mm. The ratio of branch width to fenestrule width is about 1 to 1 or 1.5. Variability of branches in 10 mm. is 9 to 12. Reverse of branches is gently convex and smooth or slightly pustulose. The obverse side is convex with a median keel bearing regularly spaced, elongated nodes.

Dissepiments are strong. Their width is normally about one half to two thirds that of the branches, with an average of 0.34 mm. Variability ranges from 0.29 mm. to 0.39 mm. Dissepiments are smooth or slightly pustulose on the reverse side and smooth or striated on the obverse. They are flush with the surface on the reverse, flush or depressed slightly below the surface on the obverse.

Fenestrules are elongate-oval to elongate-

quadrate. The length ranges from 1.0 mm. to 1.3 mm. and averages 1.1 mm. The width averages 0.52 mm. and ranges from 0.40 mm. to 0.64 mm. Variability of fenestrules in 10 mm. is 7 to 8.

Zooecial apertures are small and circular to oval. They have an average diameter of 0.07 mm. Apertures are arranged alternately, two rows on each side of the median keel and spaced at intervals of about one diameter. A thin peristome is present. Variability of apertures in 5 mm. is 18 to 20.

Median nodes are present on the obverse face. The distance between nodes averages 0.92 mm. and ranges from 0.75 mm. to 1.20 mm. Variability of nodes in 5 mm. is 6 to 7.

Zoarial Formula.—9–12/7–8//18–20/6–7.

Discussion.—This description agrees quite closely with previously published ones. Ulrich reports 9.5 to 11.5 branches, about 6 fenestrules, 18 zooecia and about 5 nodes. The Utah form differs in that the median keel is slightly weaker than previously described forms. Another difference is that the Utah form has a slightly more variable meshwork.

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

Genus HEMITRYPA Phillips 1841

HEMITRYPA sp.

Description.—Branches are strong. Their average width below a bifurcation is 0.40 mm.; above, 0.21 mm. Reverse side of branches is gently convex and smooth. The observe side is indistinct due to the presence of a reticulate network. Branches in 10 mm. number about 23 or 24.

Fenestrules are oval to elongate-quadrate. Their average length is 0.34 mm. and average width is 0.22 mm. Fenestrules in 10 mm. number 22 to 24. Dissepiments are moderately convex and smooth on the reverse, averaging 0.13 mm. in width.

Transverse and longitudinal bars on the reticulate network are about equal in width. Openings range from 0.11 mm. to 0.18 mm. and average 0.15 mm. The number of openings in 5 mm. varies from 19 to 21.

Discussion.—The fragments in my possession are too small to permit specific identification. The report is presented here mainly to record the lowest occurrence of the genus *Hemitrypa* in my collection and to assist others in recognizing it should it be found elsewhere in the west.

Occurrence.—Middle Deseret Limestone, BYU Locality 11034.

HEMITRYPA RETICULATA, Burckle, n. sp.
Pl. 132, figs. 6,7

Discussion.—The zoarium is a fenestrate expansion of semirigid branches. Intervals at which bifurcations occur could not be determined as individual fragments were not large enough to preserve two bifurcations on a single branch. The average interval is possibly in excess of 7 mm. There is no perceptible bunching of the branches near the margins of the frond.

Branches are slender. Their average width below a bifurcation is 0.57 mm.; above, 0.29 mm. Variability of branch width below a bifurcation ranges from 0.50 mm. to 0.70 mm.; above, 0.28 mm. to 0.32 mm. The ratio of branch width to fenestrule width is about 1 to 1. Variability of branches in 10 mm. is 21 to 28. Reverse of branches is strongly convex and smooth. Occasional nodes are present at the juncture of dissepiment and branch. The obverse side is strongly convex, bearing medial, regularly spaced nodes.

Dissepiments are slender. Their width is normally about two thirds that of the branches, averaging 0.19 mm. Variability ranges from 0.15 mm. to 0.26 mm. Dissepiments are smooth on either side. They are depressed on the obverse side and either depressed or flush with the surface on the reverse.

Fenestrules are quadrate to elongate-quadrate. Their length ranges from 0.38 mm. to 0.55 mm. and averages 0.43 mm. The width averages 0.27 mm. and ranges from 0.15 mm. to 0.30 mm. Variability of fenestrules in 10 mm. is 12 to 20.

Zooecial apertures are circular in outline, with an average diameter of 0.10 mm. Apertures are arranged alternately and spaced at intervals of about one diameter. The peristome is moderately well developed. Variability of apertures in 5 mm. is 18 to 24.

Median nodes are present on the obverse face. The distance between nodes averages 0.34 mm. and ranges from 0.30 mm. to 0.40 mm. Variability of nodes in 5 mm. is 14 to 20.

The obverse side is overlain by a reticulate network borne by medial nodes. The openings in the network range from 0.07 mm. to 0.12 mm. and average 0.10 mm. The network is formed by transverse and longitudinal bars, the longitudinal bars being thicker. A short node occurs at the juncture of the bars. The network is disposed so that each opening overlies an aperture on the zoarium.

Zoarial Formula.—21–28/12–20//18–24/14–20.

Discussion.—This form suggests *H. nodosa* Ulrich in its nodular growth on the reverse side of the branches. It differs, however, in being more robust and in having a more variable network. *H. nodosa* Ulrich has 11 to 12 branches in 5 mm., 7 to 8 fenestrules in 5 mm. and about 20 apertures in 5 mm.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5011.

Genus POLYPORA McCoy 1844

POLYPORA MICRONODOSA Burckle, n. sp.

Pl. 130, figs. 1,2

Description.—The zoarium is a fenestrate expansion of semirigid branches. Bifurcations occur at intervals from 1.3 mm. to 2.4 mm. in the initial stages of the frond. There is no noticeable crowding of the branches near the margins.

Branches are robust. Their average width below a bifurcation is 0.98 mm.; above, 0.47 mm. Variability of branch width below a bifurcation ranges from 0.85 mm. to 1.15 mm.; above, 0.30 mm. to 0.63 mm. The ratio of branch width to fenestrule width is about 1 to 1. In 10 mm. variability of branches is 8 to 11. Reverse of branches is strongly arched and smooth. The obverse side is gently arched with a very low median keel bearing small nodes.

Dissepiments are strong. Their width is normally about two thirds that of the branches, averaging 0.39 mm. Variability ranges from 0.26 mm. to 0.51 mm. Dissepiments are smooth and gently convex on the obverse side, and smooth and more strongly convex on the reverse. They are depressed below the surface on the obverse side, flush with it on the reverse.

Fenestrules are oval to elongate-quadrate. Their average length is 1.03 mm. Variability ranges from 0.72 mm. to 1.30 mm. The width ranges from 0.28 mm. to 0.69 mm. and averages 0.49 mm. Variability of fenestrules in 10 mm. is 7 to 9.

Zooecial apertures are small and circular, having an average diameter of 0.08 mm. They are alternately arranged and spaced

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EXPLANATION OF PLATE 131

FIG. *1,5—Fenestella rarinodosa* Condra & Elias. *1.* View showing obverse side of frond. ×5. *5.* Close-up showing details of obverse side. ×15. *2—Fenestella tenax* Ulrich. View showing obverse side side of frond. ×5.

4,6—Fenestella serratula Ulrich. *4.* Close-up of obverse side of zoarium. ×15. *6.* View of obverse side of zoarium. ×5.

3,7,10—Fenestella serratula var. *humbugensis* Burckle, n. subsp. *3.* Close-up showing the stellate processes at the apices of the nodes (a). ×25. *7.* View showing the serrate profile of the nodes. Most of the stellate processes have been removed by weathering. ×15. *10.* View showing obverse side of zoarium. ×5.

8,11—Fenestella tooelensis Burckle, n. sp. *8.* View of obverse side of frond. ×5. *11.* Close-up of obverse side. ×15. BYU Holotype No. 5004.

9,12—Fenestella parallela Hall. *9,* View of obverse side of frond. ×5. *12.* Close-up of specimen in fig. 9. ×15.

13—Fenestella hamithensis Burckle, n. sp. Close-up showing details of obverse side of frond. ×15. BYU Holotype No. 5002.

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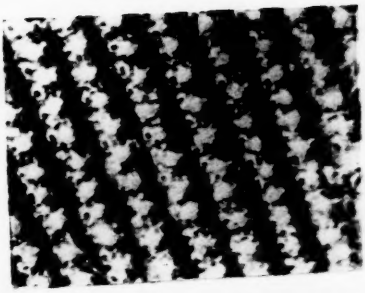

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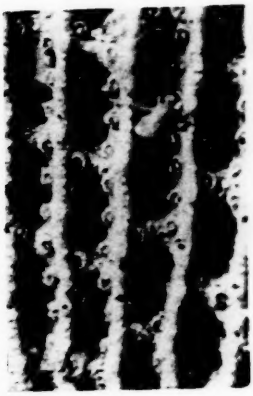

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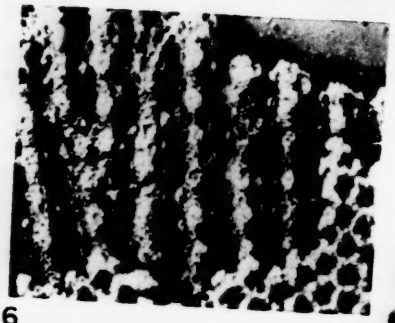

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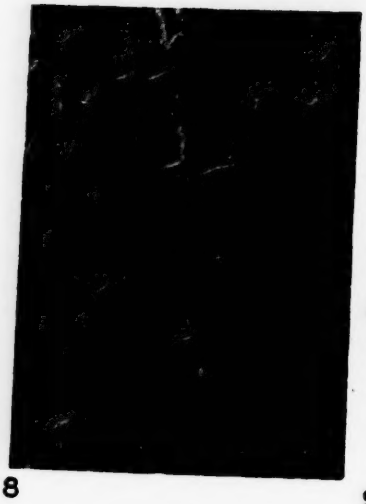

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at intervals of one and one-half to two diameters. The peristome is moderately well developed. The zooecia are arranged in rows of four to five, sometimes six, just below a bifurcation, and two to three just above a bifurcation. Variability of zooecia in 5 mm. is 16 to 21.

The median keel usually splits just above a bifurcation, the two running parallel on a branch separated by a row of zooecia. The keel bears very low nodes. The distance between nodes varies from 0.30 mm. to 0.35 mm. and averages 0.34 mm. Variability of nodes in 5 mm. is 14 to 16.

Zoarial Formula.—8–11/7–9//16–21/14–16.

Discussion.—This form appears to be intermediate between *P. tuberculata* Prout and *P. cestriensis* Ulrich. It differs from the former in having fewer branches per 10 mm. and fewer apertures per 5 mm. and from the latter in having a greater number of branches and fenestrules per 10 mm. and a greater nodal count per 5 mm.

Occurrence.—Lower Humbug formation, BYU Locality 11037.

Holotype.—Brigham Young University Specimen No. 5012.

POLYPORA STANSBURYENSIS Burckle, n. sp.
Pl. 132, figs. 2,3

Description.—The zoarium is a fenestrate flexuous expansion. The branches curve outward from the initial part of the frond and bifurcate at intervals of 3.0 mm. to 4.2 mm. There is no noticeable bunching of the branches near the margins.

Branches are robust. Their average width below a bifurcation is 1.09 mm.; above, 0.80 mm. Variability of branch width below a bifurcation ranges from 0.90 mm. to 1.20 mm.; above, 0.55 mm. to 0.99 mm. The ratio of branch width to fenestrule width is about 1 or 1.5 to 1. In 10 mm. variability of branches is 6 to 10. Reverse of branches is gently convex and smooth or striated. Obverse of branches is broadly arched, bearing median nodes but no keel.

Dissepiments are moderately strong. Their width is normally about one third to one half that of the branches, with an average width of 0.38 mm. Variability ranges from 0.25 mm. to 0.49 mm. Dissepiments are smooth on the reverse side, smooth or striated on the obverse. They are depressed below the surface on the obverse side and flush with it on the reverse.

Fenestrules are elongate-quadrate in outline. Their average length is 1.04 mm. Variability ranges from 0.90 mm. to 1.50 mm. The width ranges from 0.35 mm. to 0.72 mm. and averages 0.48 mm. Variability of fenestrules in 10 mm. is 5 to 9.

Zooecial apertures are large and circular in outline, with an average diameter of 0.12 mm. They are arranged alternately and spaced at intervals of one diameter or less. The peristome is moderately well developed. The zooecia are arranged in rows of five to six just below a bifurcation and three to four just above it. The normal figure is five below a bifurcation and three above. Variability of zooecia in 5 mm. is 13 to 15.

Median nodes are present on the obverse

EXPLANATION OF PLATE 132

FIG. *1*—*Polypora cestriensis* Ulrich. View showing reverse side of frond. ×5.
2,3—*Polypora stansburyensis* Burckle, n. sp. *2.* View of obverse side of zoarium. ×5. *3.* Close-up showing details of obverse side of frond. ×15. BYU Holotype No. 5013.
4,5—*Thamniscus raribifurcatus* Burckle, n. sp. *4* View of obverse side of frond. ×5. *5.* Close-up of a portion of the specimen in fig. *4.* ×15. BYU Holotype No. 5014.
6,7—*Hemitrypa reticulata* Burckle, n. sp. *6.* Close-up showing details of frond and reticulate network. ×15. *7.* View of obverse side of zoarium. ×5. BYU Holotype No. 5011.
8—*Polypora debilis* Elias. View showing reverse side of frond. ×5.
9,10—*Ptylopora condrai* Burckle, n. sp. *9.* View showing obverse side of zoarium. ×5. *10.* Close-up showing details of main branch and secondaries. ×15. BYU Holotype No. 5015.

face. The average distance between nodes is 0.95 mm., varying from 0.60 mm. to 2.50 mm. Variability of nodes in 5 mm. is 6 to 11.

Zoarial Formula.—6–10/5–9//12–15/6–11.

Discussion.—This species is similar to *P. micronodosa* Burckle. It differs in having larger apertures, fewer zooecia per 5 mm. and a smaller nodal count. In addition, *P. stansburyensis* Burckle does not have the median carina or exhibit a splitting of the nodes.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5013.

POLYPORA CESTRIENSIS Ulrich
Pl. 132, fig. 1

Polypora cestriensis ULRICH, 1890, Ill. Geol. Survey, v. 8, p. 594, pl. 4, figs. 4–4b; pl. 9, figs. 7–7c; KEYES, 1894, Paleontology of Missouri, Missouri Geol. Survey, v. 5, p. 29; HERNON, 1935, Jour. Paleontology, v. 9, p. 676.

Description.—The zoarium is a fenestrate expansion of semirigid branches. Bifurcations occur at intervals of 4.6 mm. to 9.8 mm. and appear to increase in number near the margins of the frond. There is no apparent bunching of the branches.

Branches are strong. Their average width below a bifurcation is 1.02 mm.; above, 0.45 mm. Variability of branch width below a bifurcation ranges from 0.90 mm. to 1.10 mm.; above, 0.40 mm. to 0.50 mm. The ratio of branch width to fenestrule width is about .75 to 1.0. Variability of branches in 10 mm. is 8 to 10. Reverse of branches is broadly arched and striated. The obverse side was not observed.

Dissepiments are strong. Their width is about one half that of branches and averages 0.35 mm. Variability ranges from 0.27 mm. to 0.40 mm. Dissepiments are convex with striations on the reverse side and either flush with the surface or depressed below it.

Fenestrules are elongate-oval with an average length of 1.77 mm. Variability ranges from 1.20 mm. to 2.50 mm. The width ranges from 0.35 mm. to 0.85 mm. and averages 0.63 mm. Variability of fenestrules in 10 mm. is 5 to 6.

Zooecial apertures are large and oval in outline. Their average diameter is 0.16 mm. They are alternately arranged and spaced at intervals of less than one diameter. Zooecia are arranged in rows of four to five just below a bifurcation and three just above. Variability of zooecia in 5 mm. is 15 to 17.

Zoarial Formula.—8–10/5–6//15–17.

Discussion.—This form differs from *P. debilis* Elias in having wider branches and dissepiments and correspondingly shorter fenestrules. It differs from Ulrich's original description in having a slightly more variable meshwork formula.

Occurrence.—Upper Great Blue limestone, BYU Locality 11033. Collected by Ronald Zeller.

POLYPORA DEBILIS Elias
Pl. 132, fig. 8

Polypora debilis ELIAS, 1957, Jour. Paleontology, v. 31, p. 421, pl. 45, figs. 4–7; pl. 48, fig. 4.

Description.—The zoarium is a fenestrate expansion of semirigid branches. Bifurcations occur at intervals of 4.20 mm. to 7.0 mm. and appear more numerous in the initial stages of the frond. There is no apparent bunching of the branches near the margins.

Branches are moderately strong. Their average width below a bifurcation is 0.80 mm.; above, 0.47 mm. Variability of branch width below a bifurcation ranges from 0.75 mm. to 0.90 mm.; above, 0.30 mm. to 0.60 mm. The ratio of branch width to fenestrule width is about 1.3 or 1.5 to 1. In 10 mm., variability of branches is 8 to 9. Reverse of branches is gently convex and striated. The obverse side is broadly arched, bearing a carina between rows of zooecia.

Dissepiments are slender. Their width is normally one third to one fourth that of the branches. The average width is 0.12 mm. Variability ranges from 0.10 mm. to 0.14 mm. Dissepiments are convex and finely striated on both sides. They are depressed below the surface on the obverse side and either depressed or flush with it on the reverse.

Fenestrules are elongate-oval, with an average length of 2.10 mm. Variability ranges from 1.80 mm. to 2.40 mm. The width ranges from 0.55 mm. to 0.80 mm. and averages 0.68 mm. The number of fenestrules in 10 mm. is 4.5.

Zooecial apertures are circular. Their average diameter is 0.08 mm. They are al-

ternately arranged and spaced at intervals of about one to one and one-half diameters. The peristome is moderately well developed. Zooecia are arranged in rows of six just below a bifurcation and four just above. Variability of zooecia in 5 mm. is 16 to 17.

Zoarial Formula.—8–9/4.5//16–17.

Discussion.—This form agrees quite closely with Elias' original description except for having slightly more branches per 10 mm. It is quite common in the Manning Canyon shale up to and including the medial limestone and is probably not too far below the point where this formation grades into the Pennsylvanian.

Occurrence.—Lower Manning Canyon shale, BYU Locality 11019. Collected by R. W. Moyle.

Genus THAMNISCUS King 1849
THAMNISCUS RARIBIFURCATUS
Burckle, n. sp.
Pl. 132, figs. 4,5

Description.—The zoarium is a long narrow stipe, branching infrequently and averaging 0.78 mm. in width, ranging from 0.60 mm. to 0.95 mm. The angle of bifurcation varies from 60 to 90 degrees. The obverse side is broadly arched, bearing zooecia surrounded by moderately prominent, undulating ridges. The reverse face is gently convex and striated. The sides of the branches are subparallel.

Zooecia are small and circular, having an average diameter of 0.09 mm. They are arranged alternately in four or five rows. The zooecia may bunch more closely and increase to six rows just prior to bifurcation. Normally, they are spaced from 1 to 1.5 diameters apart. The peristome is moderately well developed. The number of zooecia in 5 mm. is 15 to 19.

Discussion.—This species resembles *T. furcillatus* Ulrich from the Mississippi Valley. It differs in being more robust and in having more rows of zooecia on a branch (four to six verus three to five on *T. furcillatus*). *T. erectus* Elias from the Red Oak Hollow formation differs from this species in having a more acute angle of bifurcation and in having fewer rows of zooecia on a branch (three to five).

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

Holotype.—Brigham Young University Specimen No. 5014.

Family ACANTHOCLADIIDAE Zittel 1880
Genus PTYLOPORA McCoy 1844
PTYLOPORA CONDRAI Burckle, n. sp.
Pl. 132, figs. 9,10

Description.—The zoarium is pinnate. The secondary branches are slender, extending laterally from the main stem at angles ranging from 55 to 90 degrees.

The main stem is round, smooth and somewhat flexuous. Its width is almost constant around 1.50 mm. and seldom varies more than 0.30 mm. from this figure. Along a 5 mm. interval on the main branch there are five secondary branches.

Zooecial apertures are circular in outline on the main stem. Due to the poor conditions of preservation, zooecial diameters could not be obtained. However, they do appear to be large (more than 0.12 mm.). They are disposed more or less side by side in the interarea between the laterally extended secondary branches. Number of zooecia in 5 mm. is five.

The median keel is very prominent, bearing rather uniformly spaced nodes. The average width of the keel is 0.54 mm. The distance between nodes ranges from 0.90 mm. to 1.40 mm. and averages 1.10 mm.

Only a few lateral branches are present on the forms. Those that are present are usually broken off above the first dissepiment. The branches tend to flex away from the main stem. They contain two rows of zooecia and a median keel bearing a row of nodes.

Zooecia are disposed alternately with normally five to six adjoining each fenestrule. The distance between nodes ranges from 0.50 mm. to 0.75 mm. and averages 0.63 mm.

Discussion.—This form differs from previously described species in the robustness of the main stem and midrib and in the small number of nodes in 5 mm. on the main stem. As most of the specimens in my collection are incomplete it is hoped that better samples will be obtained in the future to give us a clearer picture of the nature of the secondary branches.

Occurrence.—Middle Deseret limestone, BYU Locality 11034.

Holotype.—Brigham Young University Specimen No. 5015.

PTYLOPORA ELIASI Burckle, n. sp.
Pl. 130, figs. 3,5

Description.—The zoarium is pinnate. Moderately strong secondaries branch out from the main stem at angles of 10 to 60 degrees.

The main stem is round, finely striated and either flexuous or rigid. Its width ranges from 1.10 mm. in the lower extremity to 0.75 mm. in the upper. Along a 5 mm. interval on the main branch there are five secondary branches.

Zooecial apertures on the main branch are circular and large. Their average diameter is 0.15 mm. Apertures are disposed alternately and spaced at intervals of one diameter. The number of apertures in 5 mm. is 18.

The median keel on the main branch is extremely prominent, bearing sporadic nodes. The average width of the keel is 0.38 mm. Nodes occur as small conical protuberances on the crest of the keel. Quite possibly many of the nodes have been removed by weathering.

Secondary branches form a fenestrate, flexuous expansion. Bifurcations occur at intervals of 6 mm. or more. Normally the third row of apertures is added about 3 mm. prior to bifurcation. There is no apparent bunching of the branches.

Branches are strong. Their average width below a bifurcation is 0.80 mm.; above, 0.47 mm. Variability of branch width below a bifurcation is 0.70 mm. to 0.90 mm.; above, 0.35 mm. to 0.60 mm. The ratio of branch width to fenestrule width is about 1 or 1.5 to 1. Variability of branches in 10 mm. ranges from 10 to 17. They are disposed in a zigzag manner that is almost anastomosed. Reverse of branches is gently convex and finely striated. The obverse face is convex, with a moderate to sharp median keel bearing occasional nodes.

Dissepiments are nearly obscured by encroaching zooecia. Their width is normally the same as that of the branches, with an average width of 0.71 mm. Total variability is from 0.52 mm. to 0.95 mm. Dissepiments are smooth on the obverse side and striated on the reverse. The obverse side is broadly arched and only slightly depressed below the surface. The reverse side is flush with the surface.

Fenestrules are generally oval in outline. Their length ranges from 0.71 mm. to 1.10 mm. and averages 0.84 mm. The width averages 0.43 mm. and ranges from 0.26 mm. to 0.60 mm. Variability of fenestrules in 10 mm. is 6 to 9.

Zooecial apertures are circular in outline. The average diameter is 0.15 mm. Apertures are arranged alternately and spaced at intervals of one diameter or less. The peristome is moderately well developed. Variability of apertures in 5 mm. is 16 to 22.

Median nodes are present on the obverse face. The distance between nodes ranges from 0.60 mm. to 1.40 mm. and averages 1.00 mm. Variability of nodes in 5 mm. is 2 to 6.

Discussion.—This form differs from others in its strong main stem and secondary branches. It is most like *P. prouti* Hall but differs in having fewer fenestrules and fewer zooecia on the secondary branches.

Occurrence.—Upper Humbug formation, BYU Locality 11031.

Holotype.—Brigham Young University Specimen No. 5016.

Genus SEPTOPORA Prout 1859
SEPTOPORA sp.

Description.—This form is represented by several small fragments. The primary branches are strong, averaging 0.67 mm. and ranging from 0.50 mm. to 0.78 mm. in width. Normally three to four zooecia on the primaries adjoin each fenestrule. The reverse side is convex, smooth and with scattered pores. The secondary branches are moderately strong, ranging from 0.40 mm. to 0.65 mm. and averaging 0.54 mm. They normally diverge from the primaries at angles of 35 to 40 degrees. The reverse side is smooth with scattered pores.

Fenestrules are usually oval on these specimens. The average width, from primary to primary, is 0.45 mm. and the range is from 0.41 mm. to 0.51 mm.

Zooecia are large and circular. They have an average diameter of 0.11 mm. They are arranged alternately on the primary branches and spaced about one diameter or less apart. The peristome is well developed.

The zooecia on secondary branches are placed haphazardly in two rows and spaced a diameter or less apart. Variability of zooecia in 5 mm. is 16 to 20.

Nodes are present on primary branches of the obverse face. The distance between nodes ranges from 0.50 mm. to 0.70 mm. and averages 0.57 mm. Variability of nodes in 5 mm. is 13 to 15.

Discussion.—This is a new form. However, I feel that the fragments in my collection are not large enough for good measurements or to determine the range of variability in the form. For this reason, I withhold any specific designation until such time as a more complete zoarium can be found.

Occurrence.—Lower Humbug formation, BYU Localities 11036, and 11037.

SEPTOPORA ULRICHI Burckle, n. sp.
Pl. 129, figs. 2,3

Description.—The zoarium is a coarse fenestrate expansion of rigid branches with diverging secondaries which usually coalesce with other secondaries to form a high arch convex upward.

The primary branches are strong. Their average width below a bifurcation is 0.67 mm.; above, 0.45 mm. Variability of branch width below a bifurcation ranges from 0.65 mm. to 0.70 mm.; above, 0.40 mm. to 0.55 mm. Normally three to five zooecia on the primary branch adjoin each fenestrule. The reverse side is convex and smooth with scattered pores and occasional rows of nodes on the primary branches. In 10 mm. there are 8 to 12 branches.

The secondary branches are moderately strong. They normally diverge from the primaries at angles varying from 45 to 55 degrees. The branch width averages 0.41 mm. and ranges from 0.35 mm. to 0.45 mm. The reverse of the secondaries is smooth and contains scattered pores.

Fenestrules are usually crescent-shaped, convex upward. The average width of the fenestrules, from primary to primary, is 0.70 mm. and range is from 0.40 mm. to 1.10 mm. Fenestrules in 10 mm. number from 8 to 12.

Zooecia are large and circular to oval in outline. Their average diameter is 0.12 mm. Zooecia are arranged alternately on the primary branches and spaced about one half diameter apart. Zooecia on the secondary branches are placed rather haphazardly in two rows and also spaced one half diameter apart. Normally, one aperture will occupy the center of the secondary branch. The peristome is well developed. Variability of zooecia in 5 mm. is 18 to 20.

Nodes are present on the obverse face of the primary branches. The distance between nodes ranges from 0.30 mm. to 1.00 mm. and averages 0.46 mm. In 5 mm. variability of the nodes is 10 to 16.

Discussion.—This form is similar to *S. subquadrans* Ulrich. It differs in having an indistinct keel and more nodes per 5 mm. (10 to 16 versus about 7).

Occurrence.—Lower Great Blue limestone, BYU Locality 11032.

Holotype.—Brigham Young University Specimen No. 5017.

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EXPLANATION OF PLATE 133

FIG. *1,2—Fenestella utahensis* Burckle, n. sp. *1.* View of obverse side of frond. ×5. *2.* View showing details of obverse side of frond. ×15. BYU Holotype No. 5006.

3,4—Fenestella rarinodosella Burckle, n. sp. *3.* Close-up of obverse side of frond. ×15. *4.* View of obverse side of frond. ×5. BYU Holotype No. 5003.

5,6—Fenestella regalis Ulrich. *5.* Close-up showing obverse side of zoarium. ×15. *6.* View of obverse side of zoarium. ×5.

7,8—Fenestella acarinata Burckle, n. sp. *7.* View of obverse side of zoarium. ×5. *8.* Close-up showing details of obverse side. ×15. BYU Holotype No. 5005.

9,10—Fenestella dissepinodaria Burckle, n. sp. *9.* View of obverse side of frond. ×5. *10.* Close-up showing nodes on the dissepiments. ×20. BYU Holotype No. 5007.

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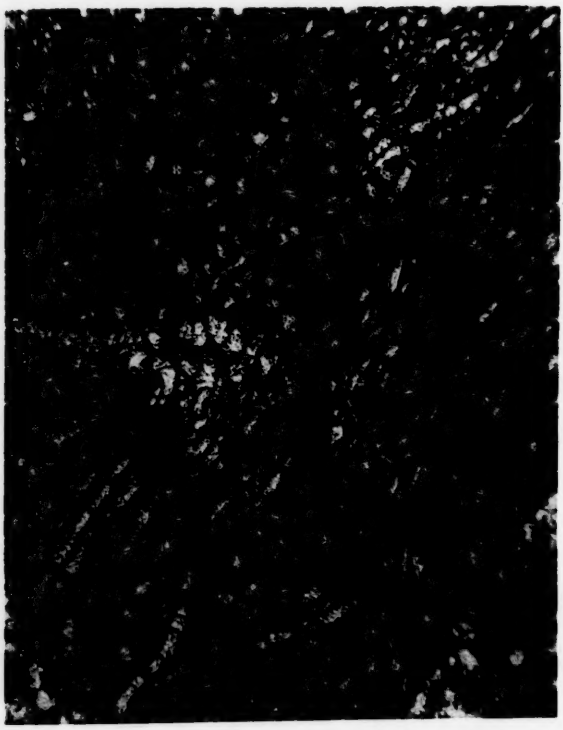

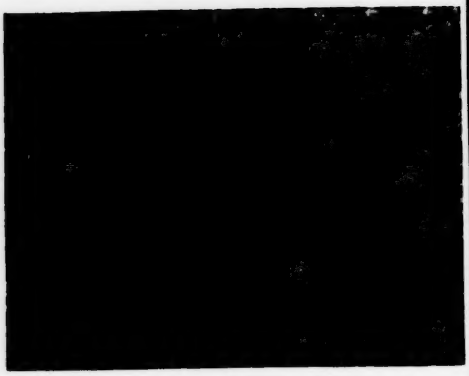

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AN INTERESTING LATE CRETACEOUS CALCAREOUS ALGA FROM GUATEMALA

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ABSTRACT—*Pycnoporidium sinuosum*, n. sp., is described from the Upper Cretaceous San Cristóbal formation of Guatemala. The species is the first known Late Cretaceous representative of this Late Jurassic-Cretaceous genus. The authors discuss the classification of genera of the Solenoporaceae of the Late Mesozoic and suggest the genus *Pycnoporidium* be excluded from the family. A suggestion is made that the genus be placed among the Siphonocladaceae of the Chlorophyceae. A probably symbiotic alga, "*Girvanella* cfr. *tosaensis* Yabe et Toyama," occurs in association with *P. sinuosum*.

INTRODUCTION

THE purpose of this paper is to describe a new calcareous alga, *Pycnoporidium sinuosum*, from the Upper Cretaceous San Cristóbal formation of eastern Guatemala. This is the first record of the genus from North America, and the first report of a Late Cretaceous species. The relationship of the genus *Pycnoporidium* to the Solenoporaceae is discussed.

The authors wish to express their gratitude to the Compañia Guatemala California de Petroleo and to the Signal Exploración de Guatemala, particularly to H. V. Kaska and Lloyd C. Miller, for their kindness in supplying the material for study and for their permission to publish the results. The junior author is grateful to the Fulbright Commission, the Colorado School of Mines Foundation, Inc., and the Japan Society for their support of this study.

STRATIGRAPHIC NOTE

The specimens containing the alga concerned were "collected by Mr. Edward Garrett from Derecho E-80, about 19.2 km. N. 81°W. Livingston and 3.8 km. S. Rio Sarstun, Departamento de Izabal, Guatemala. The locality is about 600 m. from the top of the San Cristóbal formation of Upper Cretaceous age (American usage)" (letter from Kaska dated April 29, 1958). The locality is designated as U.S.G.S. Paleobotany locality D979.

The San Cristóbal formation was named by Ver Wiebe (1925) "for 1300 to 3300 feet of sandstone, marl, limestone, and dolomite overlying the Tuxtla formation" (Imlay, 1944, p. 1016). "The most common fossils in the San Cristóbal formation are rudistids including forms reported to range from upper Turonian to Maestrichtian (Müllerried, 1936, p. 37–39; 1942b, p. 476–77;

EXPLANATION OF PLATE 134

FIG. *1–4*—*Pycnoporidium sinuosum* Johnson & Konishi, n. sp. Late Cretaceous of Guatemala. *1*, Section (U.S.G.S. number a814) (×50) through a mass of *P. sinuosum* showing the tightly packed algal filaments. *2*, Detail (U.S.G.S. number a813) (×100) showing the character of the branching and the septa or cross partitions. *3*, Another detail (U.S.G.S. number a815) (×100) showing the filaments and the septa. *4*, A section (U.S.G.S. number a 816) (×40), nearly perpendicular to the filaments, showing cross sections of the filaments.

5—A section (U.S.G.S. number a817) (×100) clearly showing the fine tubes of *Girvanella* between the coarse filaments of *Pycnoporidium*.

MacGillavry, 1934)" (Imlay, *ibid.*). Kaska's recent study (personal communication dated October 21, 1958) revealed a Campanian-Maestrichtian foraminiferal fauna from the topmost part of the San Cristóbal formation containing abundant globotruncanids and orbitoidal foraminifera. According to Kaska, "the base of the underlying Sierra Madre formation has not been found in the area from which the sample was collected, but at Hueheutenango, approximately 250 km. away, it has been dated with confidence as Aptian-Albian (more likely the latter)." So far, no detailed paleontologic zonation is possible between these dated horizons. Thus, the exact dating of *P. sinuosum*, n. sp., beyond Late Cretaceous, is uncertain.

REPOSITORY OF TYPE SPECIMENS

All the illustrated specimens including the holotype (a813) are kept in the U.S.G.S. algal collection (a813–a817), Denver Federal Center. The rest of the specimens examined are among the J. H. Johnson algal collection at the Colorado School of Mines, Golden.

SYSTEMATIC DESCRIPTIONS

Class CHLOROPHYCEAE Kützing, 1843
Order SIPHONOCLADALES (Blackman *et* Tansley) Oltmans, 1904
Family SIPHONOCLADACEAE Schmitz, 1879
Genus PYCHOPORIDIUM Yabe *et* Toyama, 1928

Pycnoporidium YABE ET TOYAMA, 1928, p. 146–149, pl. 20, fig. 3; pl. 21, figs. 1–5; pl. 22, fig. 1; PIA, 1931, p. 15; ——, 1939, p. 743, 754; PFENDER, 1939, p. 5–6.
(= *Solenoporidium* PFENDER, 1930, p. 153).

Generic range.—Late Jurassic to Late Cretaceous. (A *Pycnoporidium*, *P. toyamai* Endo [1956, p. 226, pl. 27, fig. 1, pl. 28, fig. 3], from Permian strata, Saitama Prefecture, Central Honshu, Japan, is excluded from this discussion because the present authors doubt its generic assignment.)

Type species.—*Pycnoporidium lobatum* Yabe *et* Toyama (1928, p. 146–149, pl. 20, fig. 3; pl. 21, figs. 1–5; pl. 22, fig. 1).

Repository.—Holotype; Institute of Geology and Paleontology, Tohoku University, Sendai, Japan.

Type locality.—Tochikubo formation ("Torinosu limestone" facies), Kitazawa Soma-gun, Ibaraki Prefecture, the Abukuma Mountainlands, Central Honshu, Japan.

Accredited species.—*P. lobatum* Yabe *et* Toyama (Late Jurassic of Japan and Spain, and Lower Cretaceous of Arabian Peninsula); *P. melobesioides* (Pfender) (Late Jurassic-Early Cretaceous of France); *P. melobesioides* (Pfender) (Late Jurassic-Early Cretaceous of France); *P. sinuosum* Johnson *et* Konishi (Late Cretaceous of Guatemala).

PYCNOPORIDIUM SINUOSUM Johnson & Konishi, n. sp.
Pl. 134, figs. 1–4

Description.—The thallus is an amorphous lump composed of sinuous filaments which are laterally coherent and laxly interwoven; cross sections of filaments are polygonal in the proximal part, forming loose clusters distally, or, occasionally, remaining coherent with the development of lobed tentaculae, 10 to 15 μ thick, which run approximately perpendicular to the mother filaments; the filaments are 27 to 60 μ in diameter, variously partitioned by septa at irregular intervals (ranging from 47 to 111 μ), and branched irregularly and sparsely, generally in a secund manner; the septa are 4 μ thick; the walls of the filaments are fairly thick, leaving uncalcified hollows in the middle of filaments; the diameter of these hollow tubes ranges from 25 to 35 μ; the narrow interspaces between adjacent filaments at distal part often occupied by a symbiotic (?) schizophycean alga.

Comparison.—*P. sinuosum* is readily distinguished from the other two species of the genus, *P. lobatum* and *P. melobesioides*, which have dichotomous branching "at more or less definite levels . . . giving rise to a feeble trace of concentric structure." (Yabe & Toyama, *ibid.*, p. 146). The strong sinuosity of the filaments is also a distinguishing characteristic of the new species.

An unnamed alga described under *incertae sedis* from the Upper Domerian of South Haut-Atlas, Morocco, by LeMaitre (1935, p. 50–51, pl. 12, fig. 3) might be related to *Pycnoporidium*, if it is not a *Cayeuxia*. LeMaitre mentioned that ap-

parently no septation developed; however, she also mentioned a similar form from the same locality with septation, and this, perhaps, is a *Pycnoporidium*. (This possible *Pycnoporidium* is also associated with fine filamentous alga [Schizophyceae?] [cfr. LeMaitre, pl. 12, fig. 3].) A detailed comparison of *P. sinuosum* with the Moroccan forms is impossible without quantitative data on the latter.

Discussion.—The growth habit of the new species is unknown. It is presumed, however, to be similar to that of *P. lobatum* which Yabe & Toyama (*ibid*, p. 146) described as " . . . Thallus segmented or lobed . . . attached to a substratum with more or less contracted base, by means of a thin common filament. . . . "

The thallus is an elaborated erect type (Fritsch, 1935). The prominent features of the genus are revealed in the nature of the filaments: (1) irregularly spaced septation, (2) secund nature of the branching (which occurs infrequently), and (3) development of the tentaculae. This last feature was described by Yabe & Toyama as follows for *P. lobatum:*

> " . . . interspaces between the filaments . . . transversed by a system of numerous flexuous, irregularly branching lacunae, which appear as if having been occupied by fine filaments, narrower than in direct connection with the ordinary filaments" (p. 146).

As discussed later in this paper, the three characteristics of the filaments mentioned above lead to the conclusion that the genus *Pycnoporidium* should be excluded from the Solenoporaceae and placed in the Siphonocladaceae.

Possible symbiotic relations.—Symbiosis between algal species is not uncommon. Several examples of symbiosis between fossil algal species have been reported by various authors. One of the best known examples, which may be analogous to the present case, is "*Mitcheldeania gregaria*," a Lower Carboniferous "species," which, after the careful restudy by Wood (1942), is now considered to be a mixture of three algal species, *Garwoodia gregaria*, *Girvanella* sp., and *Bevocastria conglobata*. These species make a nodular growth form with mutual interweave. It is not always decisive to prove whether the relationship is really symbiotic, merely commensal, or even parasitic. A consistent association throughout the various localities where a form is found may lead to the assumption of a symbiotic relationship.

In the case of *P. sinuosum*, it was found that the interspaces between the filaments at the distal part of the thallus are occupied by a *Girvanella*-like tubular organism with very fine diameter (7 to 8 μ) (Pl. 134, fig. 5). The same relationship is observed in the specimens of *P. lobatum* from the "Torinosu limestone" of Shikoku in the Japanese Islands. The tiny filaments occur separately in the form of pellets within the same rocks and even in rocks which do not contain *Pycnoporidium* in both the Japanese and Guatemalan localities. Yabe & Toyama (*ibid*, p. 151) named this organism *Girvanella tosaensis*. The Guatemalan form appears to be smaller in diameter; however, it is tentatively compared with the Japanese species, as *G.* cfr. *tosaensis*.

It is interesting to note that the parts of the thallus of *Pycnoporidium* attached to these filamentous algae seem to have their wall structure obliterated. This might be the case in a parasitic relationship.

Occurrence.—Guatcal locality no. 3328 (U.S.G.S. locality D979), about 600 meters below the top of the San Cristóbal formation. Although all the available specimens are from this one locality, a widespread distribution of the species in the formation is anticipated.

Suggested ecology.—The present authors have not been in the field nor have they been informed about the detailed stratigraphy of the San Cristóbal formation. Therefore, no theory as to the paleoecological implications of this occurrence of *P. sinuosum* is advanced here.

A suggested ecology may probably be seen by comparing *P. sinuosum* with the Recent allied alga, *Cladophoropsis membranaceae*, which is found in Florida, the Virgin Islands (Børgesen), the Canary Islands (Børgesen), and Hawaii (Egerod), all areas in tropical seas where the isocryme is usually above 20°C. In the Virgin Islands, this Recent species is found in shallow water, in a depth of about 10 meters (Børgesen, 1913, p. 48), both in sheltered and in more exposed places.

TAXONOMIC POSITION OF GENUS *PYCNOPORIDIUM*

When Yabe & Toyama (1928) established the genus *Pycnoporidium*, they did not refer it to any specific class of algae. Pia did not express an opinion on this genus in his 1930 review of the Solenoporaceae and Corallinaceae, but he later (1939) decided to place it among the Solenoporaceae.

The original definition of the family Solenoporaceae Pia (1927, p. 97–98) was very vague:

> ". . . Die Gesamtform der Solenoporen ist knollig. Das Zellgewebe erinnert im ganzen entschieden an Lithothamnien, doch sind die Querwaende oft recht undeutlich. Der Nachweis von Fortpflanzungsorganen ist meiner Meinung nach bisher nicht gelungen. Es ist mir wahrscheinlich, dass sie ueberhaupt nicht in den Thallus versenkt waren, sondern oberlaechlich lagen, wie bei den Squamariaceen. Deshalb scheint es mir auch night moeglich, *Solenopora* zur Familie der Corallinaceae zu stellen, selbst wenn man die Verwandtschaft fuer erwiesen haelt. Es ist wohl das beste, eine Familei zu errichten, die allerdings mit den Corallinaceen und Squamariaceen eine engere Gruppe bilden duerfte."

The validity of this family has been a matter for argument by paleophycologists for a long time. A few authorities have suggested the Solenoporaceae be merged with the Corallinaceae. The present authors, however, are of the opinion that "there are some appreciable differences between the Solenoporaceae and Corallinaceae, and . . . the differences between the two groups are still more than adequate to justify their separation" (Johnson & Konishi, 1959, p. 145 and Table 2 in Part III). A revised diagnosis of the family may be given as follows:

Family SOLENOPORACEAE

Diagnosis.—A family of red calcareous algae having a compact tissue. Cells are relatively large, commonly rectangular in longitudinal section and polygonal in cross section. Solenoporaceae commonly develop as nodular or hemispherical masses, but both thin crustose types and branching forms are known. The tissue is undifferentiated, or but slightly differentiated, into hypothallus and perithallus.

Possible reproductive structures are rarely observed and are not well known.

Discussion.—In 1943, Pia studied a Cretaceous calcareous fossil, *Cordilites cretosus* (Reuss), which he placed among his Solenoporaceae. The monotypic genus was named by Pocta as early as 1887 on the basis of *Chaetites cretosus* Reuss (1846, p. 63) in the belief that it was a coral. Pia's restudy was an important contribution to the knowledge of Late Mesozoic Solenoporaceae, for he (*ibid.*) concluded that Pocta's genus was synonymous with Yabe's *Petrophyton* (1912, p. 6–8, pl. 2, figs. 1–8, text-fig. 4), and he rejected the latter as the younger synonym of the former. *Petrophyton* was once considered by Pia (1939, p. 743, 755, etc.) to be congeneric with *Parachaetetes* Deninger (1906, p. 65–66, pl. 6, fig. 6). After examining the topotypes of *Petrophyton miyakoense* Yabe, the type species of the genus, the present authors support Pia's conclusions except for one point. Since the genus *Cordilites* was founded as a genus of Anthozoa, the algal genus *Petrophyton* should be kept valid according to the codes of international nomenclature.

It has also been suggested (Yabe & Toyama, *ibid.*, p. 141; Pia, 1930; and others) that *Petrophyton* is synonymous with *Lithocaulon* Bornemann (*non* Meneghini). Høeg (1932, p. 84) doubted this, but since the generic name, *Lithocaulon*, was preoccupied by a Tertiary alga (Meneghini, 1857, p. 550) from Sardinia, Høeg (*ibid.*) accepted this synonymy as the "most convenient way out of difficulty" (p. 84).

As Høeg pointed out, his *Petrophyton kiaeri* from the Ordovician of Norway apparently resembles Bornemann's *Lithocaulon antarcticum* (Richter, 1925, p. 542–45, pl. 6, figs. 1–4, pl. 7, figs. 1–5) from the Cretaceous of Ushuaia, Tierra del Fuego, South America, rather than Yabe's *Petrophyton miyakoense* from the Cretaceous of Japan. The present authors tentatively place both *Lithocaulon antarcticum* Bornemann and *Petrophyton kiaeri* Høeg in the genus *Parachaetetes* Deninger until a projected comprehensive revision of the family Solenoporaceae can be made. It is always possible that *Lithocaulon antarcticum* Bornemann actually is a *Petrophyton*, because different parts of the same thallus could show different microstructures, some parts being "*Lithocaulon*" and some parts being "*Petrophyton*." A careful restudy of the type

specimens of *Lithocaulon* should be made before any definite conclusion is drawn.

The genus *Pseudolithothamnium* Pfender (1936) has an encrusting growth habit and "jet d'eau" structure (like feathers of a quill) which are more or less comparable with some *Lithophyllum*. *Pseudolithothamnium*, however, has no differentiation of hypothallus and perithallus and is characterized by having very small polygonal cells in association with regularly disposed sporangia (?), 60 to 80 μ high and 40 to 55 μ wide. These internal structures as well as its habit of growth are completely different from those of *Pycnoporidium*. The monotypic species, *Pseudolithothamnium album*, is known from the Santonian of the Carpathes Mountains (Slovaquie), the Upper Cretaceous of Provence, the lower Santonian and Danian of the Pyrenees, and the Upper Cretaceous of Cuba (Keijzer, 1945), as well as from localities in the Oligocene (or Upper Eocene). Pfender placed the genus in the Solenoporaceae, but the present authors strongly doubt this assignment because of the unique microstructure of the tissue of *Pseudolithothamnium*.

There are two Tertiary genera which have have been placed among the Solenoporaceae, *Solenomeris* Douvilleé (1924, p. 169) and *Elianella* Pfender et Basse (1947, p. 275–78, pl. 12). According to Pfender and Basse (1947, p. 278), *E. elegans* occurs in the Upper Cretaceous of the Carpathian Mountains, although its exact locality is uncertain. The present authors are inclined to consider this genus as a synonym of *Parachaetetes*. Elliott (1955, p. 128) suggested the possible synonymy of *E. elegans* with *Parachaetetes asvapatii* Pia (1936).

The genus *Solenomeris* Douvillé has an encrusting habit of growth and includes three species, *S. o'gormani* Douvillé, *S. douvillei* Pfender (1926, p. 328–29, pl. 12), and *S.* (?) *douvillei* Narayana Rao *et* Varma (*non* Pfender) 1953, p. 21–22, pl. 2, figs. 10–12). This last form, which is from Pakistan, has an invalid specific name, and the present authors propose to name it *Solenomeris pakistense*, n. sp. Conceptacles have been reported from this Pakistani *Solenomeris*.

Thus, it is seen that the Late Mesozoic Solenoporaceae are now considered to be represented by the following *bona fide* genera:

Petrophyton Yabe (= *Cordilites* Pocta, 1887)—Turonian, Cenomanian, Albian, and probably Gault.

Parachaetetes Deninger, 1906—Ordovician to Cretaceous, (or early Tertiary).

Pseudochaetetes Haug, 1883—Ordovician to Cretaceous.

Solenopora Dybowski, 1878—Cambrian to Eocene.

From the above discussion, it should be evident that the family Solenoporaceae does not include any representatives which have very loosely packed "filamentous cells" such as are seen in *Pycnoporidium*. All the genera of the Solenoporaceae have a compact tissue. The Corallinaceae, which are considered to be descendants of the Solenoporaceae, have no structures similar to those of *Pycnoporidium*, either. Septation of filaments is not necessarily restricted within these families of the Cryptonemiales.

The Codiaceae or Siphonales include some calcareous forms in Recent tropical and temperate seas which resemble *Pycnoporidium* morphologically, but which do not have the septation seen in this Late Mesozoic alga. It is impossible to refer *Pycnoporidium* to the Dasycladaceae, which are another lime-depositing group in the Recent seas, because of differences in the internal construction. Thus, the authors have to find the affinities of *Pycnoporidium* among the non- or very feebly calcareous Recent marine algae. The potential ability of such feebly calcified algae as *Cladophora*, *Chaetophora* and the Vaucheriaceae to be carbonate builders has been mentioned by Pia (1926, p. 143–147, text-figs. 72–74; 1931, p. 32). However, the first two genera are nonmarine and the last group, belonging to the Xanthophyceae of the Chrysophyta, has some marine forms and some fresh-water or even terrestrial forms. The aquatic form of *Vaucheria* develops characteristic sporangia, swellings of the distal ends of the filaments, which are not observed in *Pycnoporidium*.

Among many possible affinities, the suggestion may be made that the genus *Pycnoporidium* be compared with representatives of the order Siphonocladales, which consists of three tropical families, Valoniaceae, Siphonocladaceae, and Boodleaceae. In

particular, the genus *Cladophoropsis* Børgesen (1905) of the family Siphonocladaceae considerably resembles *Pycnoporidium*.

The original diagnosis of *Cladophoropsis* given by Børgesen (1905, p. 288) is as follows:

> "Thallus a clump of filiform axes divided at irregular intervals by transverse septa; lateral branches issuing from distal end of mother cell and remaining in open communication with it; branching irregular, usually secund, often sparse; basal attachment of thallus a rhizoidal holdfast; adventitious holdfasts frequently formed on decumbent portions of thallus" (translated by Egerod, 1952, p. 355).

These diagnostic features, as far as the preserved structures of *Pycnoporidium* are concerned, are well shown in this Mesozoic alga. *Cladophoropsis* is particularly characterized by the fact that "no walls (=septations) are present at the base of the branches, these being always in open connection with the mother cells" (Børgesen, 1913, p. 44). This important feature also occurs in *Pycnoporidium*. In addition, the similarity of the ecological niches of these two genera should be mentioned.

A very close relation between the two genera is beyond doubt; however, there are differences between them which must be mentioned: (1) *Pycnoporidium* has much thicker cell walls, particularly at the distal part, and (2) it has filaments much smaller in diameter than those of *Cladophoropsis*. The first feature may merely represent a secondary thickening of the cell wall around the primary ones, and the difference in cell dimensions cannot be of generic rank. Nevertheless, because of the long missing linkage between Recent *Cladophoropsis* and its possible Cretaceous ally, and because of the lime-encrusting nature of the latter, the authors would keep the generic name of *Pycnoporidium* for the Late Mesozoic alga.

It is not too surprising to find lime-depositing ancestors of Recent algae which do not deposit lime at all. The significance of lime-encrustation in calcareous algae is still unknown. It may have some phylogenetic significance, or it may be a matter of no phylogenetic importance. Perhaps it is hazardous to refer any fossil calcareous alga to one of the three or four Recent, marine, lime-depositing families, and it is possible, as another working hypothesis, that a search for the affinities of fossil algae in the noncalcareous algae would be as constructive as the conventional line of search. If paleophycologists are to contribute to solving the phylogenetic problems of algae, such a reevaluation of their fundamental philosophy may be a necessary first step.

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THE BRACHIOPOD GENERA *INGELARELLA* AND *NOTOSPIRIFER* IN THE PERMIAN OF QUEENSLAND

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ABSTRACT—The genera *Ingelarella* and *Notospirifer* are widespread throughout the Permian of eastern Australia. Previously described species now assigned to these genera are examined. Eight new species are described from the Springsure shelf and the northern end of the Bowen basin: *I. plica*, *I. plana*, *I. ingelarensis*, *I. magna*, *I. mantuanensis*, *I. pelicanensis*, *I. havilensis*, and *N. minutus*. All species are found to have a very restricted stratigraphic range. Alternative correlations to those in current use are suggested.

INTRODUCTION

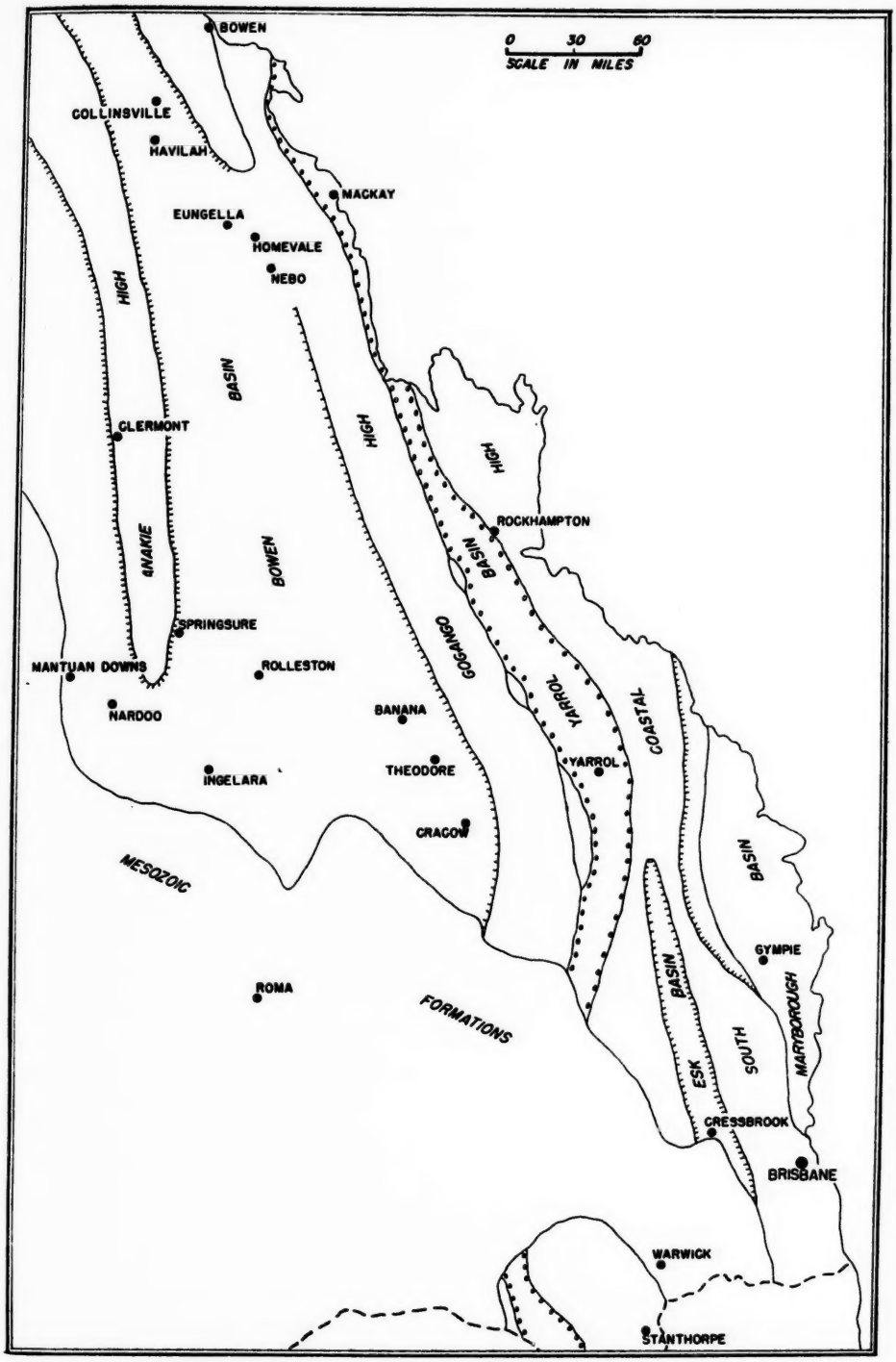
IN 1959 I reinterpreted the genus *Notospirifer* Harrington, and erected the new genus *Ingelarella* for species of the type customarily placed in *Martiniopsis subradiata* (Morris) or *M. oviformis* (McCoy). Over a period of several years I have been able to examine specimens belonging to these genera from almost every known locality in Queensland, and have had access to the collections of the University of Queensland, the Geological Survey of Queensland, the Queensland Museum, Shell (Q'ld.) Development, Australian Oil Exploration, Ltd., and Australian Associated Oilfields, Ltd.

The species described in this part of the work come from the Springsure shelf, mainly in the Serocold Anticline but also from near Mantuan Downs, and from the northern end of the Bowen basin. The Permian rocks of these two areas were the first in the State to be mapped in detail, and since the successions are relatively complete, they have come to be regarded as standard sections. However, due to the lack of detailed palaeontological studies, the correlation of these two successions was very unsatisfactory until recently when Maxwell proposed broad correlations based on the distribution of the genus *Strophalosia*. The present work supports Maxwell's interpretations in a general way, but there are differences in detail. Unfortunately no continuous correlations can be effected due to the fact that there are thick sequences of unfossiliferous rocks in both areas, and also to the equivalence of fresh water deposits in the Springsure area with marine deposits in the Bowen basin.

I am indebted to the officers of the above mentioned oil companies for stratigraphical data and the loan of specimens; to J. H. Woods of the Queensland Museum, and A. K. Denmead and H. Cribb of the Geological Survey of Queensland, for the loan of specimens; to R. F. Isbell for permission to publish on a species which he had described in manuscript; and to E. J. Webb for stratigraphical data.

STRATIGRAPHY

Springsure Shelf.—Marine Permian strata outcrop on both east and west sides of the Anakie Axis (Hill, 1951). The outcrops on the east are best developed in the Serocold Anticline, a structure first mapped by Reid (1930), and subsequently remapped in much greater detail by geologists of Shell (Queensland) Development Pty. Ltd. Webb and Patterson (Webb, 1956) have recently modified the Shell interpretation of the southern part of the anticline, now known as Reid's Dome, the region from which most of the present specimens have been collected. According to these authors, the Staircase Sandstone is absent from the Reid's Dome area. The Sirius and Dilly Shales of the northern area correspond to the Cattle Creek Shale in the south, the Staircase Sandstone "presumably having pinched out." Whether or not there is a disconformity within the Cattle Creek Shale is not made explicit, but the faunal homogeniety



TEXT-FIG. *1*—Map of southeastern Queensland showing major basins of Permian deposition and localities from which collections of ingelarellinids have been made.

throughout the complete unit suggests there is none.

The only ingelarellids from the Dilly Shale to come to my notice were too poorly preserved to permit specific identification.

From the Cattle Creek Shale in the Reid's Dome area both *I. plia* and *I. plana* have been collected in fair abundance from the ferruginous siltstones and sandstones overlying the *Eurydesma* bed of Reid. In addition, a single badly worn specimen of *Notospirifer* is known. It will be commented on later when dealing with the faunas from the eastern side of the Bowen basin. Farther north, in the Staircase Range area, both *I. plica* and *I. plana* are known from the Sirius Shale, where they are in association with a typical Cattle Creek assemblage. Important from the point of view of correlation with the Bowen basin was the discovery by Reid (1930) of a small number of specimens of *Ingelarella* in a bed right at the base of his Gypseous Marine Stage (now the Sirius Shale) in Staircase Creek. This occurrence also will be dealt with later.

The bulk of the specimens from the Ingelara Shale come from the type section in Dry Creek, Ingelara, where there are two quite distinct faunas. The base of the formation is sandy and concretionary, and contains an abundance of *Ingelarella ingelarensis*, *I. angulata*, the gastropods *Platyteichum* and *Warthia*, and the pelecypod *Glyptoleda*. The higher parts consist mainly of calcareous mudstones with *I. mantuanensis* and a rich fauna of bryozoa, tabulate corals, and small brachiopods in restricted beds (Campbell, 1953).

Notospirifer has not yet been discovered in the Mantuan Downs Formation, and *Ingelarella mantuanensis* is not common.

On the western side of the Anakie axis the Permian rocks are mainly terrestrial in origin and the lower parts are glacial. The only marine unit is the Mantuan Downs Formation which crops out widely and is very fossiliferous. Numerous specimens of *I. mantuanensis* have been obtained from it, particularly in the vicinity of Nardoo and Mantuan Downs Stations.

Bowen Basin: Western Limb in region of Parrot and Rosella Creeks.—Isbell (1955, p. 10–14) has discussed the stratigraphy of the Marine Series, and has given a generalized stratigraphical column for this area. The lowest representatives of *Ingelarella* are a few specimens of *I. ingelarensis* from the basal 20 feet of the Big *Strophalosia* Zone. The upper 70 feet of this zone contain more abundant specimens of *I. mantuanensis*. As will be shown subsequently, *I. ingelarensis* ranges up into beds thought to be equivalent to the Catherine Sandstone on the eastern flank of the Bowen Basin. Hence, using the evidence of this group alone, the Big *Strophalosia* Zone could be correlated with either the Ingelara Shale or the Catherine Sandstone of the Springsure Shelf. There are no distinctive Ingelare elements in the associated fauna however, and a correlation with part of the terrestrial Catherine Sandstone seems to be indicated. From his study of the distribution of *Strophalosia*, Maxwell (1954) concluded that the Big *Strophalosia* Zone is a condensed sequence, being equivalent to the whole sequence

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EXPLANATION OF PLATE 135

All figures approximately natural size.

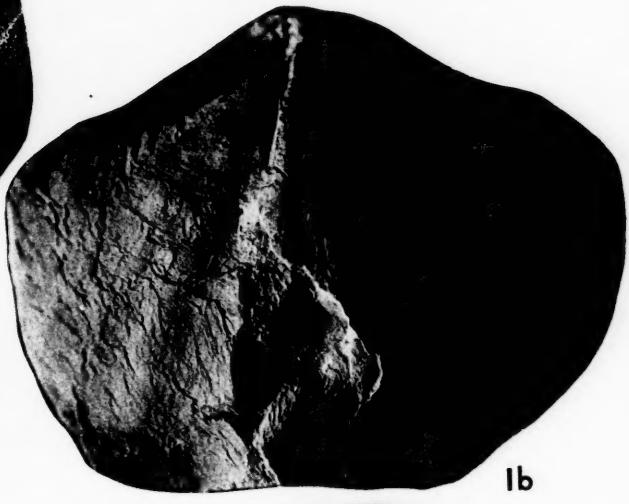
FIGS. *1–3*—*Ingelarella ingelarensis* Campbell, n. sp. *1a–c*, anterior, dorsal and ventral views of holotype, F.14170 U.Q. The dorsal adminicula are slightly longer than they appear to be in *1b*, their anterior edges not having been excavated. *2*, ventral view of partial internal mould, F.14168 U.Q. from type locality. *3*, internal mould of a brachial valve showing dorsal adminicula and muscle scars, F.24842 U.Q. from type locality.

4–5—*Ingelarella pelicanensis* Campbell, n. sp. *4a–b*, ventral and dorsal views of an internal mould, F.2075 U.Q. *5*, anterior view, F.2074 U.Q. Both specimens from type locality.

1a

2

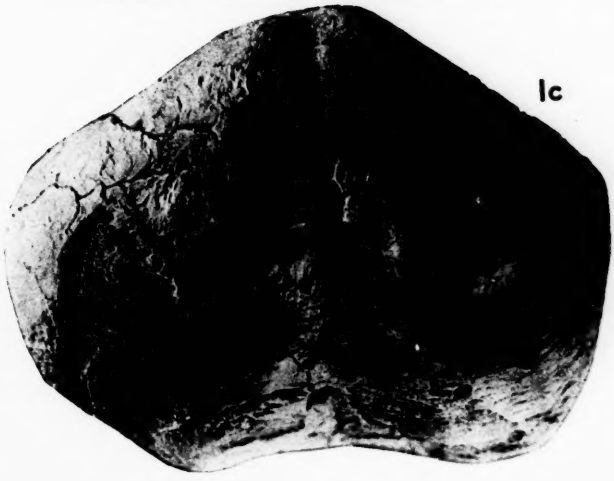
3



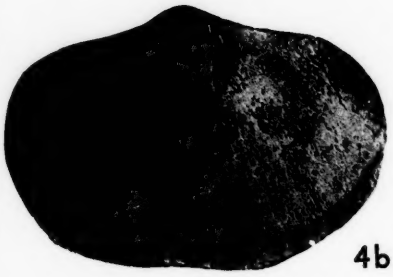
1b

4a

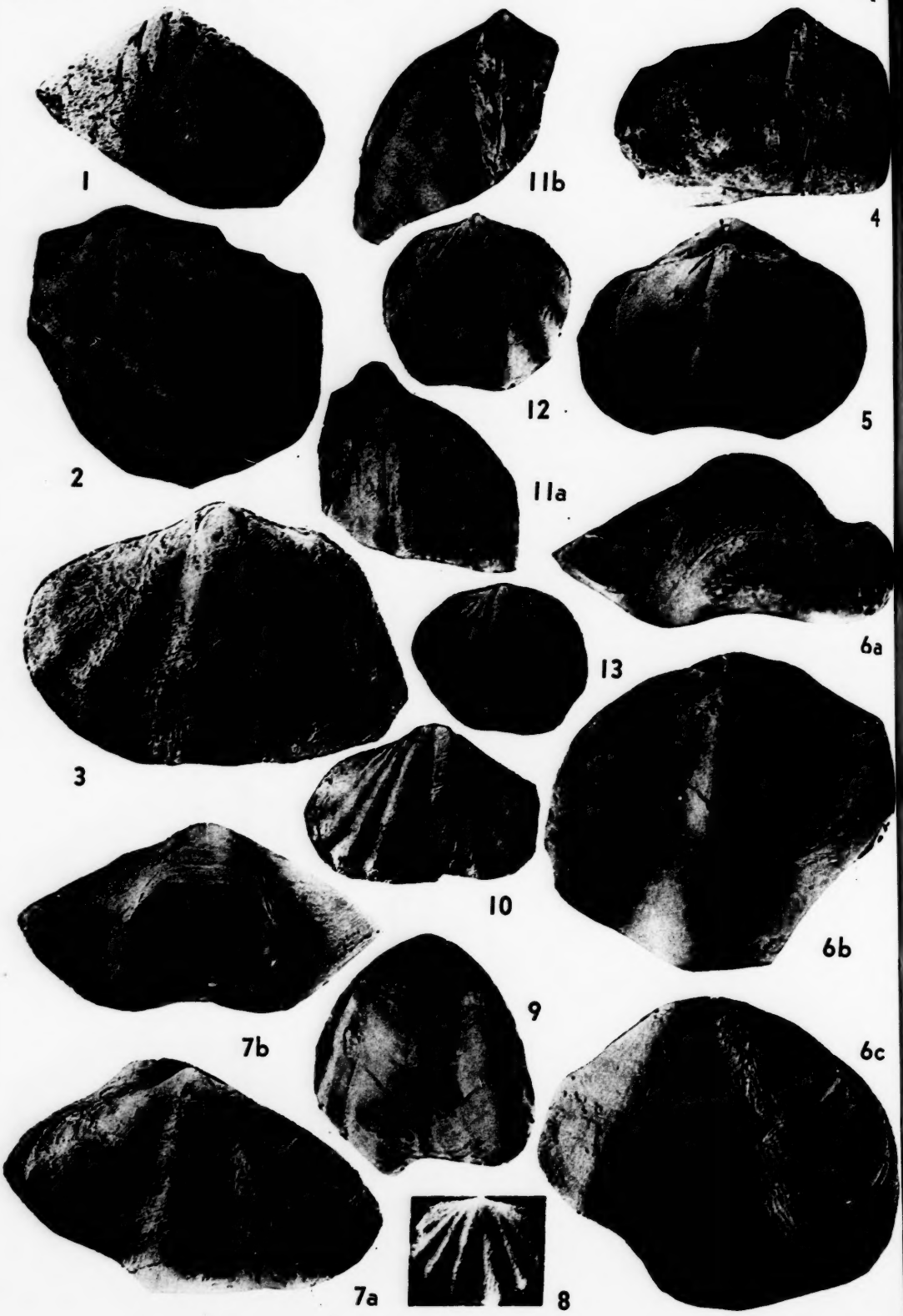
5



1c



4b


1
11b
4
2
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11a
6a
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13
10
6b
7b
9
6c
7a
8

from the Ingelara Shale to the Mantuan Downs Formation. The evidence for this is not conclusive, since at that time no *Strophalosia* was known from beds correlated with the Catherine Sandstone.

The *Streptorhynchus pelicanensis* Zone usually contains no ingelarellinids, but on the left bank of Rosella Creek two and a half miles south east of Havilah several specimens of *Notospirifer minutus* have been obtained. The latest known species of *Ingelarella* in Queensland, *I. havilensis*, comes from 300 feet above the *S. pelicanensis* Zone in Parrot Creek.

Bowen Basin: Collinsville Area.—Although marine fossils are known through most of the Middle Bowen Series in this area, ingelarellinids have been found only in the upper part of the series. This is in marked contrast to the position farther south in the Bowen Basin where the lower parts contain a profusion of both *Ingelarella* and *Notospirifer*.

Some 200–500 feet below the Big *Strophalosia* Zone is a ferruginous sandstone with numerous shelly specimens of *I. magna*, an easily recognisable species which should be useful in mapping. The Big *Strophalosia* Zone itself contains *I. mantuanensis*, and on a horizon near or in the *Streptorhynchus pelicanensis* Zone there are numerous specimens of *I. pelicanensis*. Neither *I. pelicanensis* nor *I. magna* is known from other areas.

PREVIOUSLY DESCRIBED AUSTRALIAN SPECIES

Dr. Ida Browne of Sydney is at present engaged on a revision of the Permian Spiriferacea of southeastern Australia, and hence in this work I have undertaken neither the redescription nor the designation of lectotypes or neotypes of any previously described species from that area. I have, however, examined the existing types of these species, and where possible have obtained topotypes, in order to provide an adequate basis for the comparison of the new species herein described.

The earliest species of the group to be described was *Spirifer subradiata* Sowerby 1844, which was collected by Darwin in the Hobart district during the voyage of the "Beagle." In spite of continued enquiries I have been unable to locate the types of this species, and they appear to be lost, together with the Bryozoa (Crockford, 1941, p. 397) and certain others of the Brachiopoda (Hill, 1950, p. 18) of the Darwin Collection. No precise locality was given for the types, but from the record in the "Voyage of the

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EXPLANATION OF PLATE 136

All figures natural size.

FIGS. *1–7*—*Ingelarella plana* Campbell, n. sp. *1*, internal mould of the umbo of a pedicle valve, F.25723 U.Q., from type locality. *2*, internal mould of brachial valve, F.21960 U.Q., from Staircase Creek, just south of the Springsure-Rolleston Road. *3*, partly exfoliated brachial valve, F.4745 U.N.E., from type locality. *4*, internal mould of the umbo of a pedicle valve, F.21971 U.Q., same locality as fig. *2*. *5*, partly exfoliated young shell, F.4750 U.N.E., from type locality. *6a–c*, anterior dorsal and ventral views of holotype, F.15686 U.Q. *7*, dorsal and anterior views of F.4746 U.N.E. from type locality.

8–13—*Ingelarella plica* Campbell, n. sp. *8*, a small brachial valve, F.25724 U.Q., from type locality. *9*. internal mould of part of a pedicle valve, F.15692 U.Q., from type locality. *10*, posterior part of a pedicle valve, F.4747 U.N.E. *11a–b*, dorsal and ventral views of posterior part of an internal mould, F.15693 U.Q., from type locality. *12*, a brachial valve, F.25725 U.Q. from type locality. *13*, internal mould of young brachial valve, F.25726 U.Q., from type locality.

TEXT-FIG. 2—Stratigraphic columns showing the horizons from which the various species come.

Beagle" and the statement in "Geological Observations" that "These mountains, in their lower half, are generally encased by strata containing numerous small corals and some shells. These shells have been examined by Mr. G. B. Sowerby, and are described in the appendix;" it is clear that they most probably came from the lower slopes of Mt. Wellington. Subsequent mapping has revealed a thick section of Permian rocks in this area, and ingelarellinids are recorded from numerous horizons (Voisey, 1938; Lewis, 1946; Banks & Hale, 1957). Faulting has brought a number of different horizons down to positions which could be described as the lower slopes.

Sowerby's description of the species was as follows, "*Spirifera*, Testâ laevissimâ, parte medianâ latâ, radiis lateralibus utriusque lateris paucis, inconspicuis."

"The breadth of this shell is rather greater than its length. The rays of the lateral surfaces are very few and indistinct, and the medial lobe is uncommonly large and wide."

No figure accompanied this description, and no indication of the nature of the preserving medium was given.

The next author to use the name *Spirifer subradiata* was Morris, who in 1845 referred several specimens from the Hobart area and the South Coast of New South Wales to the species. Morris explicitly states that he did not have access to Sowerby's specimens (p. 281), and an examination of casts of his (Morris') specimens shows that his interpretation of the species was very broad, the four figured specimens (including two from Mt. Wellington) representing four distinct species by present standards. Each of the Tasmanian specimens could be described in Sowerby's terms. Subsequent authors have used *S. subradiata* to cover almost the complete range of ingelarellinids, and as currently used the name is devoid of any significant zoological or stratigraphical content.

Due to the kindness of M. R. Banks, and G. Lane of the University of Tasmania and J. de Bavay and A. H. Voisey of the University of New England, I have been able to examine specimens from several localities in the Hobart area and have reached the conclusion that there are at least two and probably three species to which Sowerby's description could be applied. At the present it appears to be impossible to identify this species positively and to designate the original locality and horizon. I am satisfied, however, that none of the Queensland species described herein is identical with any of the species from the Hobart area to which Sowerby's diagnosis could apply.

Morris in 1845 also described the species *Spirifer darwini*, the types of which are in the British Museum of Natural History. This species has been discussed recently (Campbell, 1959).

D'Orbigny (1846) in D'Urville's "Voyage au Pôle Sud," figured what is probably an *Ingelarella*, almost certainly from the Hunter Valley of N.S.W., as *Spirifer hombronianus*. No description was given. I have not found material comparable with his figures in my collections.

The next species described was *Spirifer strzeleckii* de Koninck 1877. Before him, de Koninck had specimens from several localities in the Hunter Valley. His description is apparently composite, externals being described from specimens of one type and internals from specimens of another, as is shown by reference to the number of plicae and the presence of a median furrow on the fold. His specimens were destroyed by fire in 1886, but the specimens from the Permian of Gympie, Queenland, referred by Etheridge Sr. (1872, p. 330, pl. 16, figs. 3–5) to *Spirifer undifera* var. *undulata* Römer, and placed by de Koninck in his synonymy, are now housed in the Queensland Museum (catalogue numbers F. 946, F. 3272, and possibly F. 3273). Having examined these, I am convinced that they are definitely not conspecific with either of the types figured by de Koninck, and since they do not appear to have been used in drawing up the original description, they do not qualify as syntypes. A neotype will have to be erected, but judging from de Koninck's figures this will not affect the validity of any of the new Queensland species.

Etheridge (1892, p. 239) introduced the names *morrisi*, *transversa* and *koninckí* as varieties of *Martiniopsis? subradiata* Sowerby. It is clear that he intended the specimen of *Spirifera subradiata* of Morris 1845, pl. 15, fig. 5, to be taken as typical of *morrisi*. "I propose to distinguish by the above varietal name those forms of *M. subradiata* in which the longitudinal measure-

ment is at least equal to the transverse, and at times exceeds it, giving rise to an oval outline. Such a variety is represented by the figure of Morris quoted above." This specimen is now in the British Museum, labelled B. 8542. In any case, this specimen is the only one available for selection as lectotype, since of the other specimens which were mentioned in the original description only those from Cania are still in existence, and these were regarded as abnormal (see explanation of pl. 11, figs. 12–13). The Copenhagen Decisions (Art, 31, para. 137(3), p. 73) specifically recommend that such specimens should never be chosen as lectotypes. Morris' specimen is comparable with those herein referred to *I. ingelarensis*, but may be distinguished from them by its greater relative length, stronger plicae, and more strongly defined limits to its median fold.

The variety named *transversa* by Etheridge (de Koninck pl. 12, fig. 16) appears from the nature of the closely packed aggregated growth lamellae to be merely an aberrant variant. A very similar transverse individual has been observed in the population from the *Martiniopsis* Beds of the Eight Mile Creek Block near Warwick, where it is clear that the individual is merely an aberrant. In view of this, and the fact that de Koninck's specimen was destroyed in the Garden Palace Fire, I am permitting the name *transversa* Etheridge to lapse.

For the specimens referred by de Koninck to *Spirifer darwinii* Morris, Etheridge (1892, p. 239) erected the varietal name *Martiniopsis subradiata* var. *koninckı*. The three specimens figured by de Koninck probably represent three distinct species, but since all the specimens have been destroyed it is impossible to confirm this. Of the specimens figured, that on pl. 11, fig. 10 and 10a, is similar to, but nevertheless distinguishable from, a species from Mr. Britton, but neither of the others has a Queensland representative.

Etheridge (1919, p. 185) described a number of diverse specimens from the railway cuttings at Farley and Branxton as *Martiniopsis subradiata* var. *branxtonensis*. I have examined specimens from these localities and am convinced that a number of species is represented. Some of the Farley specimens are close to *I. plana* Campbell, n. sp.

SYSTEMATIC DESCRIPTIONS

INGELARELLA PLANA Campbell, n. sp.
Pl. 136, figs. 1–7

Holotype.—F. 15686 U.Q. Coll. from Cattle Creek Shale, in Cattle Creek, 2 miles from the junction with Consuelo Creek; paratypes F. 15687–8 and F. 21962–F. 21973 U.Q. and F. 5000–1 U.N.E.

Diagnosis.—The shells are medium sized and somewhat flattened, with a very broad sinus of medium depth in the pedicle valve, produced into a high slightly flattened tongue anteriorly; the commissure is parasulcate; the umbonal cavities are only slightly thickened; ventral adminicula diverge at a low angle along the floor of the valve; dorsal adminicula are wedge shaped, extending one quarter to one fifth of the total length of the valve.

Description.—The anterior profile of the shell is flattened, the ratio height: length: width being approximately 5:8:10 in the holotype; some other specimens are proportionately wider and higher; the pedicle valve is very gently convex, the greatest convexity being toward the umbo; the cardinal area measures from one half to three quarters of the maximum width of the valve; the median sinus is exceptionally broad, its floor rounded and posteriorly bearing a shallow median groove; the sinal angle of the holotype about 42°, while that of four paratypes ranges from 35° to 40°; the sinus is produced into a large, slightly flattened and gently concave tongue anteriorly; the anterior profile of the lateral slopes is flat or slightly concave; the slopes are evenly and gently convex towards the umbo, but anteriorly develop a depression of variable depth marginal to the fold bordering the sinus; the linear depressions are spaced 125–140 per 25 sq. mm. on the posterior part of the sinus of the holotype, with very faint traces of discontinuous striae between the depressions (Campbell, 1959, pl. 56, fig. 10).

The brachial valve has a high pointed umbo; the fold is high and rounded posteriorly, and either rounded, flattened or even slightly furrowed toward the front; the fold is bordered on either side by a change of

TABLE 1—DIMENSIONS OF REPRESENTATIVES OF *Ingelarella* AND *Notospirifer* (c. = circa)

Length (mm.)	Width (mm.)	Height (mm.)	Length Brachial Valve (mm.)	Height Fold (mm.)	Length Pedicle Muscle Field (mm.)	Width Pedicle Muscle Field (mm.)	Single Angle	Length Length Dorsal Adminicula (mm.)
				INGELARELLA PLANA				
—	c. 72	—	—	—	c. 30	7	—	19
—	c. 72	—	43	15	—	—	—	—
—	c. 68	—	—	—	—	—	—	14
c. 45	c. 66	33	38	13	—	—	38°	—
c. 50	c. 62	28	43	16	—	—	42°	—
c. 42	c. 60	—	—	—	21	6	—	—
—	c. 51	—	—	—	15	8	—	—
c. 36	47	c. 23	c. 31	c. 10	—	—	40°	8
				INGELARELLA INGELARENSIS				
c. 75	88	c. 50	c. 62	—	32	14	—	21
70	75	c. 45	c. 60	16	—	—	—	—
62	82	49	53	c. 22	—	—	24°	21
60	65	41	55	c. 15	28	11	22°	25
60	81	44	53	12	32	—	25°	18
				INGELARELLA MANTUANENSIS				
75	86	52	64	7	—	—	—	25
60	70	c. 38	55	5	—	—	20°	22
c. 46	c. 50	—	—	—	21	9	20°	—
3. 38	c. 40	—	c. 33	—	c. 13	6	—	—
				INGELARELLA HAVILENSIS				
—	c. 78	c. 44	—	—	30	12	—	25
—	c. 78	—	—	—	34	19	—	—
c. 67	77	—	c. 60	—	—	—	19°	24
60	c. 68	37	50	c. 10	—	—	20°	—
—	c. 60	—	c. 52	—	—	—	—	22
—	55	—	40	7	—	—	—	20
				NOTOSPIRIFER MINUTUS				
24	34	—	—	—	—	—	27°	—
17	28	c. 15	15	—	—	—	23°	—
16	c. 25	—	14	3.5	7.5	4.5	18°	—
14	c. 24	9.5	13	3	8	3.5	26°	—
13.5	c. 22	10	12	2	7	2.5	24°	—
13	20	—	10.5	2	7	3.5	26°	—

slope which is scarcely distinguishable at the umbo, but which becomes broader and deeper anteriorly, until at the margin it is troughlike; the lateral slopes outside these marginal areas are narrow, and in the holotype occupy less than one half of the total surface of the valve; the lateral slopes are almost smooth to distinctly uniplicate.

Interior.—The umbonal cavities of the pedicle valve are slightly thickened; adminicula are elongate and only slightly divergent along the floor of the valve; adminicula are always thin where they meet the dental lamellae, but become strongly thickened toward the shell wall; the dental lamellae are slightly thickened.

The cardinal process is small for a shell of this size; the umbonal cavities are not at all thickened; the adminicula are wedge shaped, and one quarter to one fifth of the total length of the valve; the adductor scars and descending lamellae and sockets were not observed; the specimen is small, with about twenty volutions in each spire.

Remarks.—The holotype is the only virtually complete undistorted specimen obtained from the type locality. The above description has been based on this specimen with details added from seven topotypes and eight other incomplete paratypes.

Localities and horizon.—This species occurs rarely in the Cattle Creek Shale of the Springsure area. Whitehouse's lists (1930, p. 157) record no species of this group at all from beds now considered to be of Cattle Creek age. I have collected it in Cattle Creek itself, two miles above the Junction with Consuelo Creek. Australian Oil Exploration geologists have found it at K.O.E. 7 (in bed of Staircase Creek at the first crossing of the Rolleston-Springsure Road about 13 miles by road from Springsure) in association with a typical Cattle Creek assemblage.

INGELARELLA PLICA Campbell, n. sp.
Pl. 136, figs. 8–13

Holotype.—F. 25725 U.Q. from the Cattle Creek Shale, in Cattle Creek, two miles from the junction with Consuelo Creek; paratypes F. 15691–4 and F. 25721–4 U.Q. from the type locality.

Diagnosis.—The shells are of small to moderate size and strongly biconvex; the fold and sinus both have median furrows; the lateral slopes are deeply plicate; the pedicle valve has four or five plicae on each side; ventral adminicula are strong and inflected at their tips to enclose the muscle field; dorsal adminicula are short and wedge-like.

Description.—The pedicle valve is very convex, particularly toward the umbo; the cardinal area is approximately two-thirds of the total width of the valve; the dental ridges are well developed; the median sinus is of moderate depth, its floor being angular umbonally, but flattening out rapidly about the middle of the valve; there is a shallow median groove in the sinus over its entire length; the sinal angle is *c.* 23°; each slope has four or five rounded plicae, the most lateral one being very weak; there is a small smooth region toward the cardinal extremities; the linear surface pits are well spaced and usually have a density of 120–150 per 25 sq. mm. on the anterior part of sinus, although on some bands they become more crowded; there are extremely fine discontinuous striae between the pits.

The brachial umbo is obtuse; the faintly concave cardinal area is approximately 3 mm. high; the median fold is high and carries a well developed median depression.

Interior.—The umbonal cavities are moderately thickened; free portions of the adminicula are short, strongly wedge shaped, and continued forward as low ridges to form a stout canoe-shaped structure completely enclosing the muscle field; the latter is divided posteriorly by a vertically walled ridge up to 2 mm. high and 1.5 mm. broad near the umbo, but gradually decreasing in height toward the front, and becoming indistinct midway to the anterior edge of the field; adductor scars are set in a low depression which runs the length of the whole field, the total width of the depressions being 4 mm. in a specimen about 50 mm. in width; diductor scars are on a high level and not so long as the adductors; the dental lamellae are thick.

The umbonal cavities of brachial valve are scarcely thickened; the crural plates are supported on wedge-shaped adminicula which are straight or slightly concave toward each other, and extend about one quarter the length of the valve; the central adductor scars are broad, slightly impressed; the postero-lateral scars diverge from the central pair near the posterior extremity of the latter, and have a pointed termination against the adminicula; the spires in one small specimen are 40 mm. in width with twelve visible volutions, although there could be up to twenty.

Remarks.—The material on which this species is based is neither abundant nor well preserved, and includes a number of juveniles. Nevertheless it is a very distinctive form readily separable from other coarsely plicate species known from New

South Wales and other parts of Queensland.

I have examined the two syntypes of the comparable *Spirifer oviformis* McCoy, now labelled E. 10648 and E. 10649 in the Sedgwick Museum, Cambridge. These come from Barraba, near Cessnock in the Hunter Valley, N.S.W.

The syntypes are both internal moulds, and both are imperfect. The one labelled E. 10648 is the more complete, but it has been considerably distorted and the details of the internal structures have not been well preserved. Hence it has been decided to choose E. 10649 as lectotype of *I. oviformis* in spite of the fact that a portion of the brachial valve has been removed.

The sinus of the lectotype is broad and shallow and bears a broad indefinite median depression. The sinal angle is about 32°. The lateral slopes of the pedicle valve each bear three deep plicae. The ventral adminicula are slightly divergent for most of their length, but converge anteriorly, and the muscle field is continued forward on a high narrow rounded platform. The umbonal thickening is moderate. The broad median fold of the brachial valve bears a deep rounded median groove and the lateral slopes are tri-plicate. The crural plates are strong and are supported on robust, straight, dorsal adminicula which are more than one-third the length of the valve. The estimated length is 65 mm., the estimated width 65 mm., and the estimated height 45 mm.

In the specimen E. 10648 the sinus appears to be narrower than that of the lectotype, and it bears a median fold anteriorly. Both of these features may be due to distortion. Further the dorsal adminicula are not developed as strongly as those of E. 10649 and the lateral slopes of the pedicle valve bear four plicae instead of three.

The specimens herein referred to *Ingelarella plica* differ from *I. oviformis* (McCoy) in their relatively deeper median sinus, much more marked median platform in the pedicle muscle field and their shorter and less robust dorsal adminicula.

Localities and horizon.—This form is characteristic of the Cattle Creek Shale and is known from Cattle Creek itself two miles from the junction with Consuelo Creek, and from K.O.E. 7 (see above).

INGELARELLA INGELARENSIS
Campbell, n. sp.
Pl. 135, figs. 1–3; Pl. 138, fig. 4

? *Martiniopsis subradiata* (Morris) WHITEHOUSE, 1930, Queensland Govt. Mining. Jour., v. 31, p. 157, (Verandah Creek Fauna).

"*Martiniopsis*" *sp. a.* CAMPBELL, 1953, Univ. of Queensland Papers, v. 4, no. 3, p. 10, pl. 4, figs. 1–3; pl. 5, figs. 1–3.

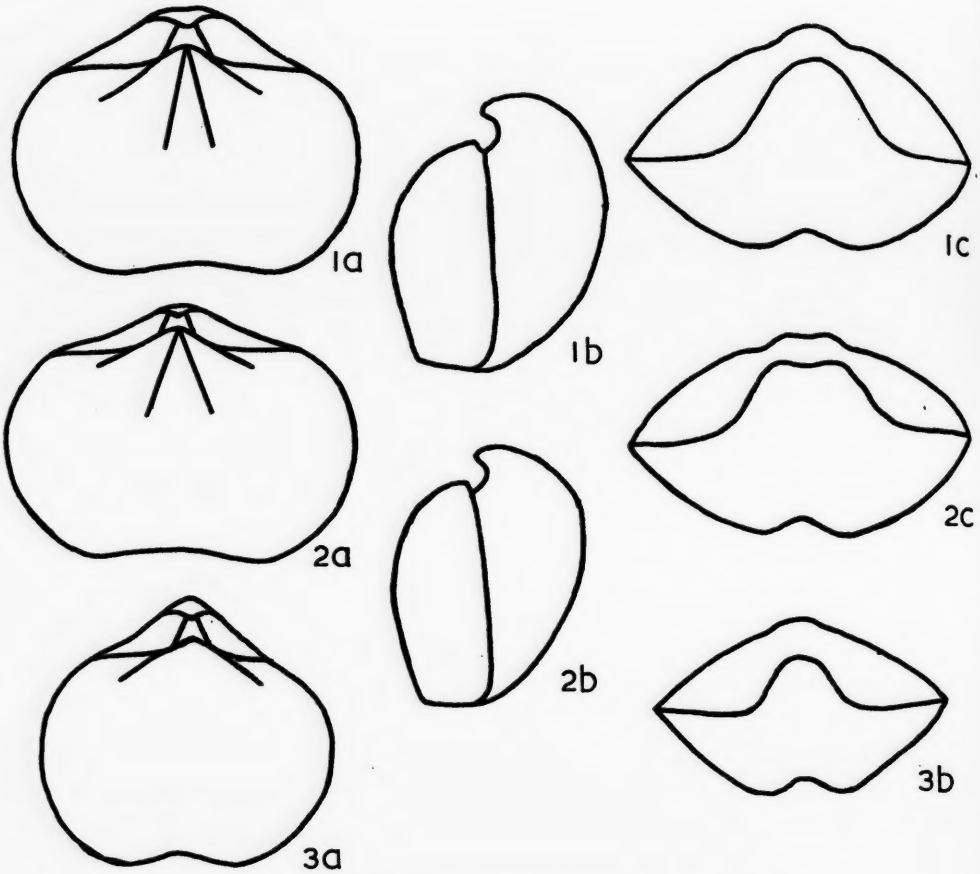
Holotype.—F. 14170 U.Q. Coll., from the Ingelara Shale; ½ mile north of the road in Dry Creek, Ingelara Station; Paratypes F. 14168, F. 15698, F. 24842 U.Q. Coll., and F. 4749 U.N.E. Coll., from the type locality.

Diagnosis.—The shell is large; the median sinus is moderately deep and produced into a relatively high tongue anteriorly; the fold is rounded and scarcely breaks the general contour of the valve; the commissure is uniplicate; the lateral slopes are smooth or almost imperceptibly plicate; the pedicle umbonal cavities are slightly thickened; dorsal adminicula are very long and slightly diverging.

Description.—Adult shells are large and strongly and subequally biconvex; specimens from the type locality vary considerably in proportions; the hinge line measures from three-fifths to seven-tenths of the maximum width of the valve.

The pedicle valve is most strongly convex toward the umbo; the cardinal area is strongly concave; the sinus is of moderate depth, inclined to be angular toward the umbo and rounded anteriorly; some specimens have a faint median groove extending the length of the sinus; the sinus of the holotype is produced into a slightly concave tongue, but in other specimens the tongue is lower and more concave; the sinal angle averages 23°; the lateral slopes are steep and gently convex, and either smooth or bearing one or two very faint plicae toward the sinus, and smooth laterally.

The umbo of the brachial valve is high and pointed, rising some 5 mm. above the hinge line; the cardinal area is markedly concave; the median fold is rounded, flattened or faintly grooved, and either rises gradually from the lateral slopes without breaking the general contour of the valve, or is delimited by a slightly flattened area on either side; the lateral slopes have very weak plicae similar to those of the

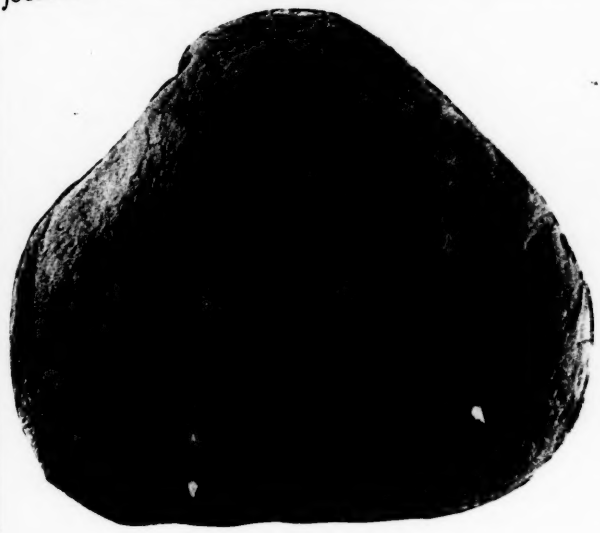


TEXT-FIG. *3*—Profiles of three specimens of *Ingelarella ingelarensis*.

EXPLANATION OF PLATE 137

All figures natural size.

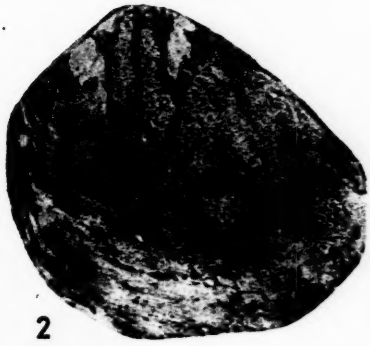
FIGS. *1–3*—*Ingelarella mantuanensis* Campbell, n. sp. *1a–d*, ventral, dorsal, anterior and lateral views of a large specimen, with the pedicle valve compressed toward the front, F.25685 U.Q., from the Mantuan Downs Fm., Nardoo. *2*, partly exfoliated pedicle valve of a small specimen, F.15669 U.Q., from the Mantuan Downs Fm., Rewan Station. *3*, posterior part of the internal mould of a pedicle valve, F.25683 U.Q., from the Mantuan Downs Fm., Nardoo.



1a

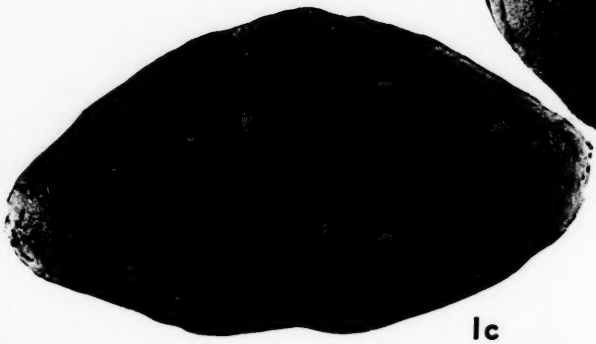
1d

1b

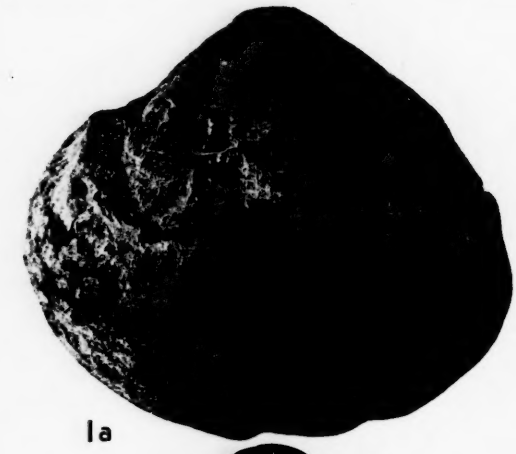


2

3



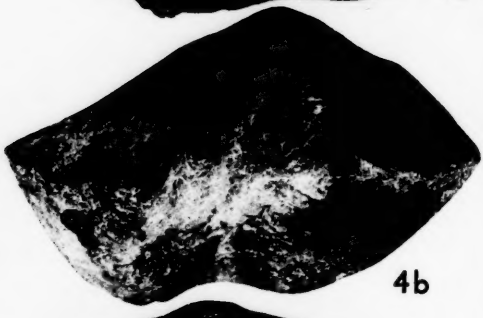
1c



1a

4a

1b

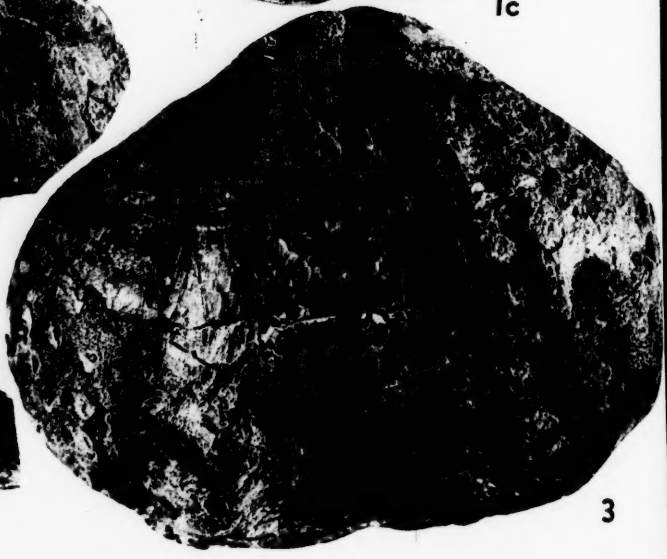


4b

1c

2a

2b



3

pedicle valve, or smooth; details of the surface ornament were not preserved.

Interior.—Thickening both of the umbonal cavities and of the adminicula is slight; adminicula are slightly divergent on the floor of the valve; the muscle field is semi-elliptical in outline and its width is two-fifths of its length.

The brachial valve has very long adminicula extending approximately one third the length of the valve; the sockets are only slightly thickened and the socket plates short; adminicula are vertical on the floor of the valve, and thin over most of their height but rapidly thicken near the shell wall; descending lamellae thin out very rapidly beneath the sockets; the spires are not well exposed on any specimen; central adductor scars are long and very narrow, and situated on slight platforms; posterolateral scars are broader, pointed posteriorly, and separated from the central pair by a furrow.

Remarks.—This species is readily separated from *I. angulata*, with which it is found associated, by its larger adult size, much less plicate lateral slopes, rounded median fold and by the less well developed groove in the sinus. From *I. plana* it is distinguished by its narrower sinus, differently plicated lateral slopes, relatively longer dorsal adminicula, and its unusual dorsal adductor field.

It is highly variable in overall proportions, the height of the fold in the commissure, the sharpness of the break between the sides of the fold and the lateral slopes, and the degree of flattening or furrowing of the fold. The variation in the number and distinctness of the plicae on the lateral slopes is noteworthy, although slight wear often eliminates all trace of them.

Localities and horizons.—At the type locality this species is moderately abundant. It is restricted to the sandstone unit in the lower part of the Ingelara Shale. South of Collinsville it is known in the lower part of the Big *Strophalosia* Zone where it occurs only sparsely.

INGELARELLA MAGNA Campbell, n. sp.
Pl. 140, figs. 1–4

Holotype.—F. 2051 G.S.Q., labelled M 137, Marine Gully, Bowen River Coalfield; Paratypes F. 2318–F. 2321, G.S.Q.

Diagnosis.—The shell is large, with a rather shallow sinus carrying a broad rounded plication anteriorly; the fold is steep sided and has a shallow median groove; the lateral slopes have three to five faint plicae; the umbonal cavities of the pedicle valve are strongly thickened; ventral adminicula are divergent; dorsal adminicula are moderately long and straight.

Description.—Adult specimens are very large, the largest being *c.* 100 mm. wide and 85 mm. long; the pedicle valve is rather flat to moderately convex, and evenly convex over its whole length; the umbo is high and strongly incurved at its tip; the dental ridges are narrow, and delthyrial angle *c.* 55°; the cardinal area is one half to three-fifths of the maximum width of the valve;

EXPLANATION OF PLATE 138

All figures natural size.

FIGS. *1–3*—*Ingelarella mantuanensis* Campbell, n. sp. *1a–c*, ventral dorsal and anterior views of holotype, F.15659 U.Q., from the Mantuan Downs Fm., Rewan. *2a–b*, ventral and anterior views of part of an incomplete pedicle valve; note the very weak sinus; F.15660 U.Q., from the Mantuan Downs Fm., Nardoo. *3*, a larger pedicle valve showing a deeper, broader sinus, and slight plication of the lateral slopes, F.15661 U.Q., from the Mantuan Downs Fm., Nardoo.

4a–b—*Ingelarella ingelarensis* Campbell, n. sp., dorsal and anterior views of a topotype, F.15698 U.Q.

the median sinus is broad (sinal angle *c.* 30°, slightly greater in the holotype), of moderate depth to very shallow, usually with sharply defined steep margins, and bears a broad, rounded fold on its anterior third; the lateral slopes are gently convex and bear three to five very faint plicae.

The brachial valve is moderately convex; the fold is steep sided and bears a shallow median depression over almost its entire length; there is a narrow flattened area on either side of the fold.

Interior.—The pedicle valve has strongly thickened umbonal cavities; adminicula are thick and wedge shaped; dental lamellae are massive and bear large hooked teeth; the muscle field reaches half the length of the valve, well raised and strongly triangular in front.

Dorsal adminicula measure about one-third the length of the valve, and are almost straight.

Remarks.—The sample from which the above description has been prepared is small (8 specimens) and the preservation leaves much to be desired. However, the specimens are so distinctive that a new specific name is clearly necessary.

Only two specimens of brachial valves are available. The above description is drawn up from a valve still attached to a pedicle valve. The second one, which is from the type locality, is more plicate on the lateral slopes than most specimens, and is strongly convex. It shows relatively long, almost straight adminicula, and large adductor scars. The central adductor scars are narrow posteriorly, and widen to their anterior edge which is abruptly rounded. The lateral scars diverge from the central pair at their mid-length, and extend 10 mm. behind them. The cardinal process is large and consists of 90–100 plates. The specimen is most probably to be referred to this species.

There is considerable variation in the depth of the sinus, and in the prominence of its median fold, but in all specimens there is a clear cut margin to the sinus. One specimen shows a shallow median groove over at least part of its length, but there is no vestige of such a structure on any other specimen. Some specimens in which the median plication in the sinus is smaller than normal are superficially similar to *I. mantuanensis*, but the thickened shoulders of the pedicle valve and the shorter dorsal adminicula distinguish them. Mr. G. Lane has shown me similar specimens from the Woodbridge Group of Tasmania.

Localities and Horizon.—All the specimens were collected by officers of the Geological Survey of Queensland. The type locality is M 137 Marine Gully, Bowen River Coalfield. Other specimens are labelled Marine Gully near Birralee Road, C.P.A. 14; and McCallums P.A. As far as can be determined at present from the unpublished maps in the Geological Survey Office, the type locality is some 200–500 feet stratigraphically below the Big *Strophalosia* Zone. The second locality is presumably very close to the first, but the position of McCallums P.A. has not been determined.

Ingelarella mantuanensis Campbell, n. sp.

Pl. 137, figs. 1–3; Pl. 138, figs. 1–3

Holotype.—F. 15659 U.Q. Coll., from the *Productus* Bed, three miles west of Rewan Homestead, Springsure district; Paratypes F. 15669–F. 15678, and F. 25683–F. 25685 U.Q. Coll.

Diagnosis.—The species includes medium to large sized shells; the sinus is shallow with a distinct median furrow; the fold is low and has a shallow median depression; ventral adminicula are long and subparallel; dorsal adminicula are long, deep, straight and slightly diverging; the umbonal cavities in both valves are only slightly thickened.

Description.—Adult specimens attain a very large size, the largest observed being approximately 100 mm. wide; the best preserved specimens are moderately biconvex, but there is considerable variation in this feature; the hinge line averages seven tenths of the maximum width of the valve.

The sinus is shallow, and in some specimens almost imperceptible, although the median furrow even in these latter forms is nearly always clear; the sinal angle is very variable (mean 23°, range 18°–28° for 5 specimens); the lateral slopes are entirely smooth or have one or two very weak plicae adjacent to the sinus; the preservation of surface pits is too poor to permit their measurement.

The brachial valve not as convex as the pedicle valve; the fold is low and well defined, with steep-sided margins and a broad shallow median depression probably running its entire length; no depressions bound the fold; the commissure is uniplicate to sulciplicate; the lateral slopes are either smooth or very faintly uni- or biplicate.

Interior.—The umbonal cavities of the pedicle valve are weakly to moderately thickened; ventral adminicula in adults are usually thick and parallel, and most often not inflected at their anterior edges; in juveniles, adminicula are weaker; the median keel dividing the posterior edge of the muscle field is often unusually long.

The umbonal cavities of brachial valve are unthickened; adminicula are up to almost half the length of the valve, and gently tapering; other features were not observed.

Remarks.—From the Illawarra district of the South Coast of New South Wales Morris (1845, pl. 16 fig. 1) has figured a specimen which he referred to *S. subradiata* Sowerby but which is very similar to *I. mantuanensis* Campbell, n. sp., in all external features but unfortunately no internal features are shown. I have examined specimens from Westley Park, Gerringong, in the Illawarra district, which agree externally with Morris' specimen, the internals of which differ from those of *I. mantuanensis* in their much more widely divergent ventral adminicula, and their shorter and very weakly developed dorsal adminicula.

I. mantuanensis can be distinguished from *I. ingelarensis* by its shallower sinus with its more distinct median furrow, more furrowed dorsal fold, much lower plication of the commissure and stronger and more nearly parallel ventral adminicula. The two species are closely related and their limits of variation approach.

Localities and Horizon.—This species is found in the Mantuan Downs Formation on both sides of the Anakie Anticline, rather rarely on the east and in the Serocold anticline, more abundantly on the west at "Nardoo." In the latter area there is considerable variability in the species, particularly in the depth of the sinus and the degree of plication of the lateral slopes. Some of the range of variation in the sinus is illustrated on Plate 138, figs. 1,2,3. In no case does the plication of the slopes become prominent. The specimens from the former locality are usually rather smaller than those from the latter.

From the upper part of the Ingelara shale several specimens closely comparable with *I. mantuanensis* have been collected. Unfortunately most of these are somewhat distorted and compressed, and since the distinction between *I. mantuanensis* and *I. ingelarensis* is based mainly on the shell form, it is impossible to decide with certainty what proportion of this population lies within the range of variation of each of these species. However, the best preserved specimens are clearly most closely allied to *I. mantuanensis.*

HOMEVALIA PELICANENSIS
Campbell, n. sp.
Pl. 135, figs. 4–5; Pl. 140, fig. 5

Holotype.—2078 G.S.Q. Coll., from C.P.A. 21, ½ mile from Eastern Boundary, Bowen River Coal Field, horizon in, or close to the *Streptorhynchus pelicanensis* Zone; Paratypes 2071–2077 G.S.Q. Coll.

Diagnosis.—The shell is small and wider than long; the median sinus is shallow and bears a median groove; the fold is low, rounded and poorly differentiated from the lateral slopes; the commissure is weakly uniplicate; the lateral slopes are smooth; ventral adminicula are strongly divergent; dorsal adminicula diverge in the umbo and become subparallel in front.

Description.—The shell is transversely oval in outline and its convexity is low, that of the pedicle valve being distinctly greater than that of the brachial valve; height: length:width ratios vary around 2:3:4.

The cardinal area of pedicle valve is gently concave toward the hinge, but the concavity increases greatly beneath the sharply incurved umbo; the median sinus is very shallow, its margins poorly defined, with a shallow groove running its entire length; the sinal angle averages about 30°; the commissure is usually weakly uniplicate, though occasionally rectimarginate; the lateral slopes are gently and evenly convex and nonplicate.

The brachial valve is about five-eighths as long as wide; the lateral slopes are gently

and evenly convex; the median fold is very low and scarcely breaks the general contour of the valve over most of its length; no specimens showing details of the surface ornament are available.

Interior.—The umbonal cavities are only slightly thickened; adminicula are approximately one-fifth of the total length of the valve, very variable in their degree of thickening, and widely divergent on the floor of the valve, with their anterior tips never incurved; the dental lamellae are relatively unthickened; very weak ridges are given off from the edge of the adminicula and bound the anterior edge of the muscel field; the median ridge dividing the posterior portion of the muscle field is very short and variable in its development; the adductor scars are narrow and extend beyond the edge of the diductors in most specimens.

Dorsal adminicula are well developed and thickened in the umbo, diverging toward the muscle scars, but they curve around the posterior edge of these structures, becoming subparallel, and extend approximately one third of the length of the valve; the muscle scars are only slightly impressed; the central pair are very narrow and the posterolateral pair derived from near their anterior edge parallel them for almost their entire length and then swing out laterally; the muscle field is divided medially by a low and narrow posteriorly keeled platform; descending lamellae and spires are unknown.

Remarks.—These specimens were collected by the Geological Survey of Queensland in 1914. Almost all are internal moulds, only one fragment of an external mould being available.

INGELARELLA HAVILENSIS Isbell MS.
Pl. 139, figs. 3–6

Martiniopsis ISBELL, 1955, Univ. of Queensland Papers, vol. 4, no. 11, p. 12.

Holotype.—F. 15797 U.Q. Coll; Paratypes F. 15798–F. 15809 U.Q. Coll.

Diagnosis.—The shells are large, with a short hinge line; the sinus is shallow but has a deep median groove; the fold is steep sided, having a deep median groove; the lateral slopes are smooth; the pedicle umbo is strongly thickened; ventral adminicula are long and slightly diverging; dorsal adminicula are long and tapering.

Description.—The shell is strongly biconvex and wider than long; the hinge line is about three-fifths of the maximum width of the shell; the pedicle umbo is incurved over a strongly and evenly concave cardinal area; the delthyrial angle is about 60°; the median sinus is quite shallow, but has an appearance of depth because of the deep median groove which it bears over its entire length; the sinus merges gradually into the gently convex. nonplicate lateral slopes; the sinal angle averages 20°.

The brachial valve is not well preserved in any specimen; the median fold is low, steep-

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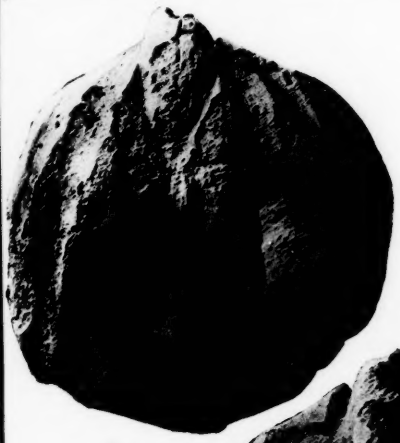
EXPLANATION OF PLATE 139

All figures natural size.

FIGS. *1a–b—Ingelarella* sp., ventral and dorsal views of one of the original syntypes of *Spirifer oviformis* McCoy, E.10648 S.M., from Barraba, N.S.W.

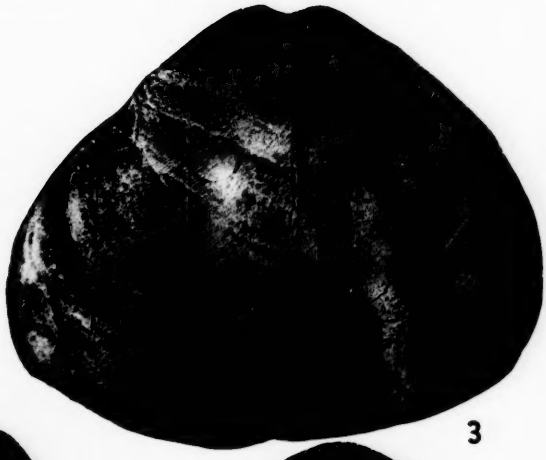
2a–c—Ingelarella oviformis (McCoy), ventral, dorsal and anterior views of the lectotype, E.10649 S.M., from Barraba, N.S.W.

3–6—Ingelarella havilensis Campbell, n. sp. *3*, ventral view of holotype, F.15797 U.Q., *4*, inal mould of posterior of a pedicle valve, F.15738 U.Q. *5–6*, internal moulds of two incomplete brachial valves, F.15788 and F.15800 U.Q. All specimens from some 500 feet below the top of the Middle Bowen Marine Series, Mulgrave Road crossing of Parrot Creek, Bowen Basin.



1a

1b



3

4

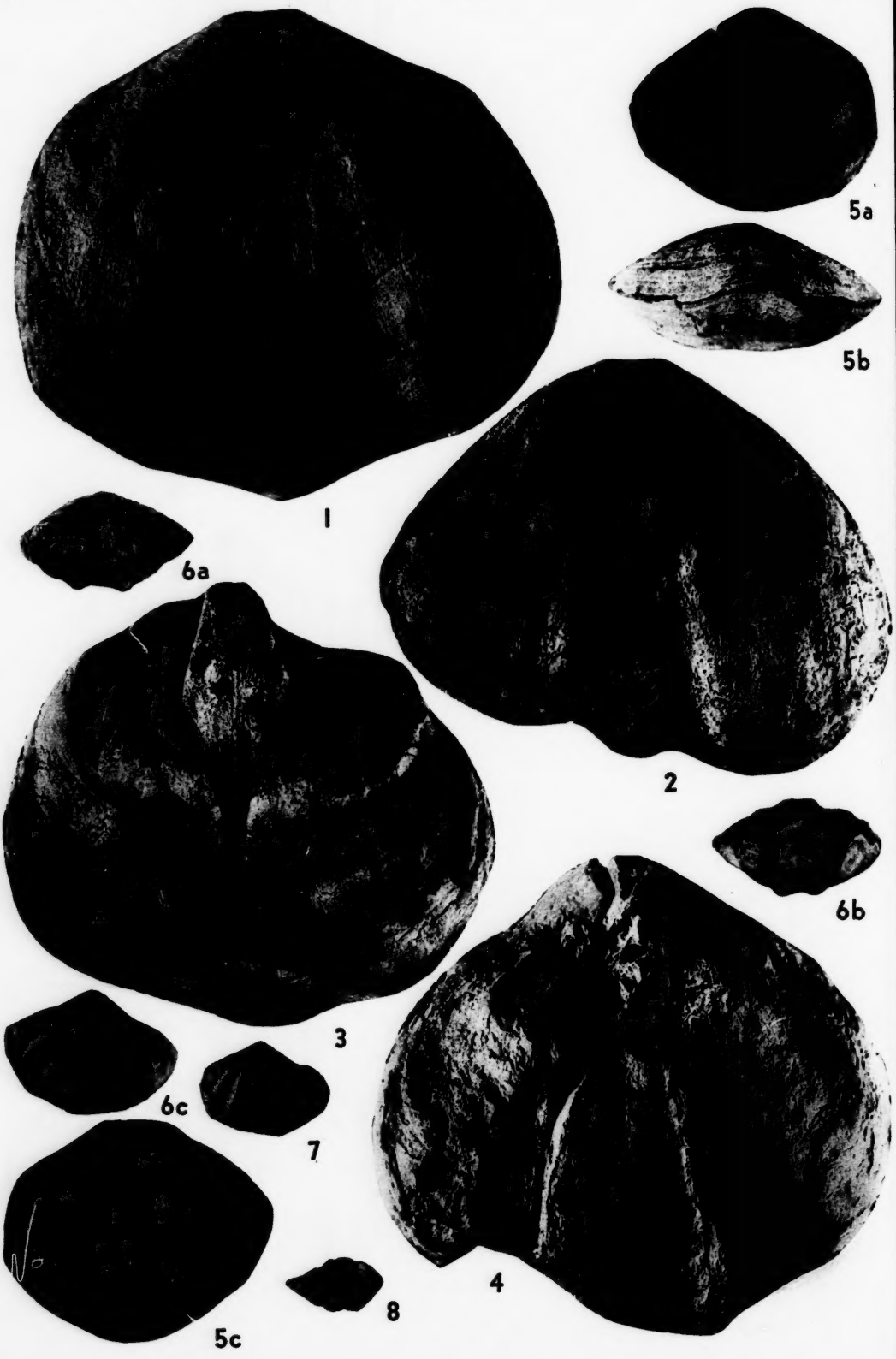
5

6

2c

2a

2b


1
5a
5b
2
6a
3
6b
6c
7
4
5c
8

sided, and with a gradually deepening median groove from umbo to commissure; the lateral slopes are gently convex and smooth; the commissure is sulciplicate; the preservation of surface pits was not sufficiently good to permit measurement.

Interior.—The pedicle umbo is greatly thickened; sometimes narrow deeply channelled umbonal cavities remain in the thickened shoulders (Pl. 139, fig. 5); the dental lamellae are thick, in some specimens enormously so, and supported on well developed slightly divergent adminicula; dental lamellae and adminicula are sometimes almost completely enveloped in the umbonal thickening; the muscle field is much longer than wide, although the width is very variable, and subtriangular in front, raised well above the general shell level; the posterior part of the adductors is sometimes situated on a high narrow platform.

The crural plates are comparatively small, supported on long straight adminicula reaching from two fifths to one half the length of the valve; the muscle scars and spires were not observed.

Remarks.—This species can be readily distinguished from *I. mantuanensis* Campbell, n. sp., by the stronger thickening of its umbo and its higher median fold, which carries a much deeper median furrow. It has apparently developed from the latter species. *I. havilensis* was discovered by R. F. Isbell who subsequently discussed it in an unpublished thesis submitted to the University of Queensland. He has kindly permitted me to include the species in the present work.

Locality and Horizon.—It is known only from the type locality, the Mulgrave Road Crossing at Parrot Creek, Bowen Basin. It lies on an horizon some 500 ft. below the top of the Middle Bowen Marine Series (Isbell 1955, p. 12). This is probably the highest horizon in Queensland from which members of this subfamily have been obtained.

NOTOSPIRIFER sp.

Remarks.—A single specimen, F. 4748 U.N.E., very poorly preserved, has been found in the Cattle Creek Shale in Cattle Creek. Its form and a small patch of deeply pitted ornament clearly indicate its generic position, but it is not possible to decide its specific affinities with conviction. It will be commented on subsequently when dealing with the faunas from the eastern side of the Bowen basin.

NOTOSPIRIFER MINUTUS Campbell, n. sp.
Pl. 139, figs. 6–8

Martiniopsis? sp. ISBELL, 1955, Univ. of Queensland Papers, v. 4, no. 11, p. 13.

Holotype.—F. 15823A/B U.Q. Coll.: from Rosella Creek two and one-half miles S.E. of Havilah Homestead, Collinsville Dis-

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EXPLANATION OF PLATE 140

All figures natural size.

FIGS. *1–4—Ingelarella magna* Campbell, n. sp. *1*, ventral view of holotype, F.2051 G.S.Q. *2*, ventral view of incomplete pedicle valve, F.2318 G.S.Q., from Marine Gully, near Birralee Rd., C.P.A.14, Bowen River. *3*, partial internal mould of a pedicle valve, F.2319 G.S.Q., from same locality, *4*, brachial view of an almost complete specimen, F.2322 G.S.Q., from McCallums P.A., Bowen River.

5—Ingelarella pelicanensis Campbell, n. sp. *5a–c*, ventral anterior, and dorsal views of holotype, F.2078 G.S.Q.

6–8—Notospirifer minutus Campbell, n. sp. *6a–c*. posterior, anterior and ventral views of holotype, F.15829 U.Q. *7,8*, ventral and anterior views of two internal moulds, F.15832 and F.15837 U.Q., both from type locality.

trict: Paratypes F. 15824–F. 15837 U.Q. Coll.

Diagnosis.—The shells are small sized and subequally biconvex; the sinus is relatively shallow; the fold is flattened on top; the lateral slopes are coarsely plicate, the pedicle valve bearing four (or occasionally five) plicae on each side of the sinus; ventral adminicula are thin and short; dorsal adminicula are very short.

Description.—The shells are small in size, transversely oval in outline, and with the maximum width at about the mid-length of the valve; the length/width ratio appears to increase with age although there are insufficient specimens to be certain of this.

The pedicle valve is most convex toward the umbo and flattens slightly toward the front; the umbo is obtuse and only slightly incurved over the gently concave cardinal area; dental ridges are moderately developed; the delthyrial angle varies from 55°–60°; the median sinus is rather flat-bottomed and has a faint median furrow toward the umbo, but tends to become rounded toward the front; the sinal angle averages 23° (10 specimens over a range of 18° to 28°); the lateral slopes are gently and evenly convex, and usually ornamented with four plicae, the most lateral of which is very slight, though sometimes with four distinct plicae and an incipient fifth; the surface is ornamented with widely spaced, coarse growth lamellae, becoming more frequent around the anterior margins.

The brachial valve is very transversely elliptical in outline; the umbo is low and obtuse; the cardinal area is orthocline and 1.5 mm. high in a specimen 17 mm. long; the fold is low and flattened, with steep sides; a weak median depression is sometimes present on the fold; the lateral slopes are either straight or very slightly convex in anterior profile; the whole surface of each valve is covered with circular pits which become progressively deeper on the adult portions; these pits are much deeper than wide, radially disposed, and project into the shell at angles between about 20° and 45° to the shell surface; the pits on the anterior of the valve have a density of about 600 per 25 sq. mm.

Interior.—The umbonal cavities are scarcely thickened; adminicula are short and slender, usually diverging posteriorly and tending to become subparallel toward the front, though sometimes straight or even more divergent toward the front; the dental lamellae are much thicker than the adminicula; the posterior margin of the muscle field is bounded by the adminicula but its anterior portion is not well defined; two plicae bound the sinus, which is continuous across the outer edges of the muscle field; the adductor scars very narrow and not always clearly differentiated.

The cardinal process is small and composed of 25–30 plates; adminicula are thin and their free portions along the floor of the valve never reach a length greater than 1 mm.; the muscle scars are not sufficiently well preserved to warrant description; a fine median ridge is present.

Remarks.—Some very fine moulds of the external surface have been preserved. When the infillings of the surface pits have been broken across, each one is seen to have a hollow core suggesting a short pustule in the centre of each pit. However these cores seem to stop short of the general surface of the shell. Thin sections of the shell show no such pustules and it is thought that the appearance of cores in the moulds is due to some peculiarity of preservation.

This is the smallest species of *Notospirifer* yet described. It is readily distinguished from the type species by its small size, deeper plication. It also differs from the other members of the genus in the great depth of the surface pits.

Locality and Horizon.—To date it is known only from the type locality, which according to Isbell (1955, p. 13) represents the structural duplication of the *Streptorhynchus pelicanensis* zone in the Upper Bowen Coal Measures.

Repositories

U.Q., Geology Department, University of Queensland, Brisbane; G.S.Q., Geological Survey of Queensland, Brisbane; U.N.E., Geology Department, University of New England, Armidale, New South Wales.

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JOURNAL OF PALENTOLOGY, V. 34, NO. 6, P. 1124–1128, PL. 141, 3 TEXT-FIGS., NOVEMBER, 1960

MISSISSIPPIAN AMMONOIDS FROM NORTHWESTERN CANADA

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State University of Iowa, Iowa City

ABSTRACT—Upper Mississippian ammonoids are recorded and described from two localities. Well preserved specimens representing *Goniatites crenistria* Phillips, an index fossil known in various parts of the world, come from the Peel River in north central Yukon Territory. A single individual described as a new species, *Prolecanites warreni* Sellers & Furnish, was secured from a well core in the Liard River area of northern British Columbia.

GONIATITES FROM THE UPPER PEEL RIVER, YUKON TERRITORY

THE genus *Goniatites* has been known for some time in northwestern Canada, but has generally received only listing. Gordon (1957) described several representatives of the genus, among them *G. crenistria*, from the Eagle-Circle District and the Brooks Range of eastern and northern Alaska. The collection under study was obtained from the Upper Peel River (Text-fig. 1) in Mississippian dark silty limestone. The specimens were sent by P. S. Warren to A. K. Miller for study in 1953.

Goniatites has considerable stratigraphic value, as it is now interpreted. In North America this genus is generally regarded as a typical fossil for lower Chesterian of the Mississippian; it is also a zone index for the equivalent Bollandian, of the British Carboniferous section.

The specimens under study occur in a dark silty limestone unit of the Upper Peel River Mississippian section, on the north bank of the river. This particular unit is relatively close to the top of the section, and bears an affinity with that described by Gordon in the Eagle-Circle District. However, in this study nothing more than an approximate correlation between the two areas can be suggested. The fact that *Goniatites* does occur in these rocks, and in rocks stratigraphically below these, indicates that an age of lower Chesterian should be assigned to them.

Genus GONIATITES DeHaan, 1825
GONIATITES CRENISTRIA Phillips
Pl. 141, figs. 1–5

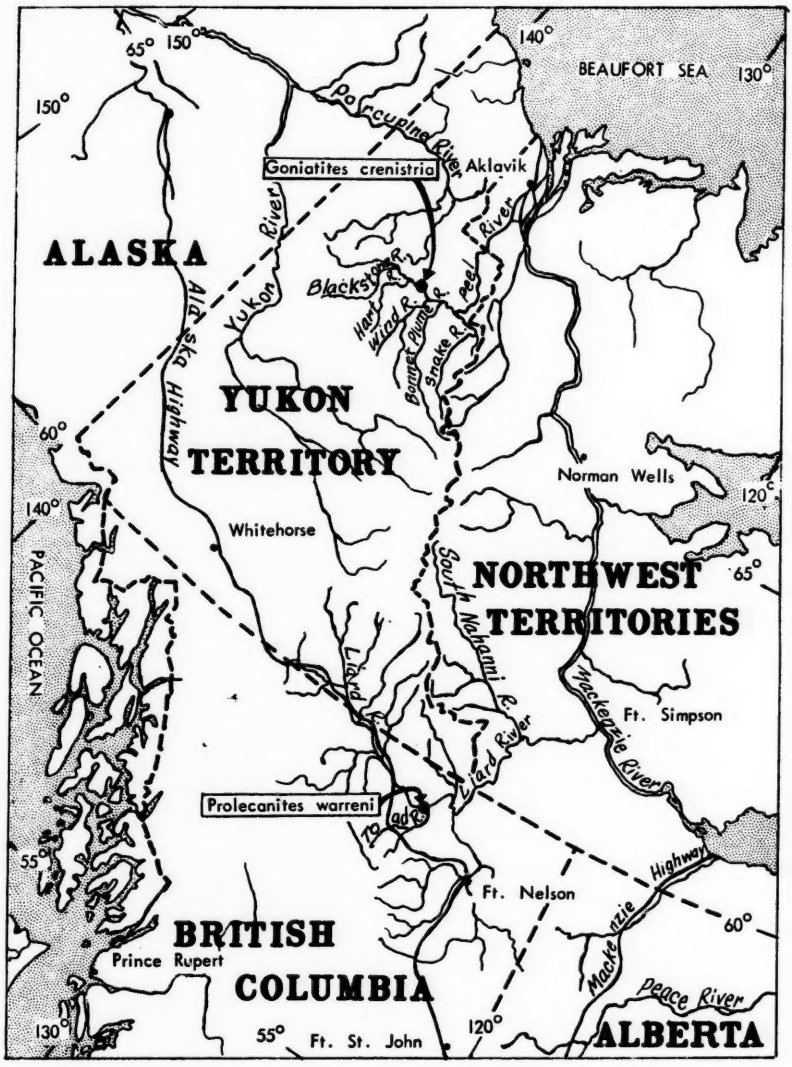
Goniatites crenistria PHILLIPS, 1836, Illustrations of the geology of Yorkshire, pt. 2, p. 234, pl. 19, figs. 7–9; BISAT, 1924, Proc. Yorkshire Geol. Soc., n. ser., v. 20, pt. I, p. 78, pl. 3, figs. 3,4; pl. 9, figs. 1,2; GORDON, 1957, Mississippian cephalopods of northern and eastern Alaska. U. S. Geol. Survey, Prof. Paper 283, p. 42, pl. 5, figs. 1–16.

Glyphioceras crenistria (Phillips) FOORD & CRICK, 1897, Catalogue of fossil Cephalopoda in the British Museum; Pt. III, p. 160, fig. 76; SCHMIDT, 1924, Die Carbonischen Goniatiten Deutschlands, Preuss. geol. Landensanst. Jahrb., Bd. 45, p. 565, pl. 21, figs. 1–3, pl. 5, fig. 1.

The shell is globose in the youthful stage, becoming subglobose to thickly discoidal in the adult. The mature shell has gently rounded sides, with well rounded ventral and ventro-lateral areas. The shell is involute, and was so during growth, the width of umbilicus being roughly one-tenth of the total shell diameter. The shell surface is crenistriate at diameter 17 mm. and larger. Transverse striae are faintly sinuous and form indistinct lateral and ventral sinuses. Some specimens possess faint longitudinal lirae. Constrictions are present on the specimens under study, two to three per whorl.

The suture consists of eight lobes and corresponding saddles, ventral and first lateral lobes with sigmoidal sides. The first lateral saddle is evenly rounded in the young (diameter 14 mm. and smaller) but becomes tapered and narrowly rounded in the adult (diameter 20 mm. and larger). The median saddle becomes progressively higher, extending to about one-third of the height of the ventral lobe in a mature specimen (Text-fig. 2A,B).

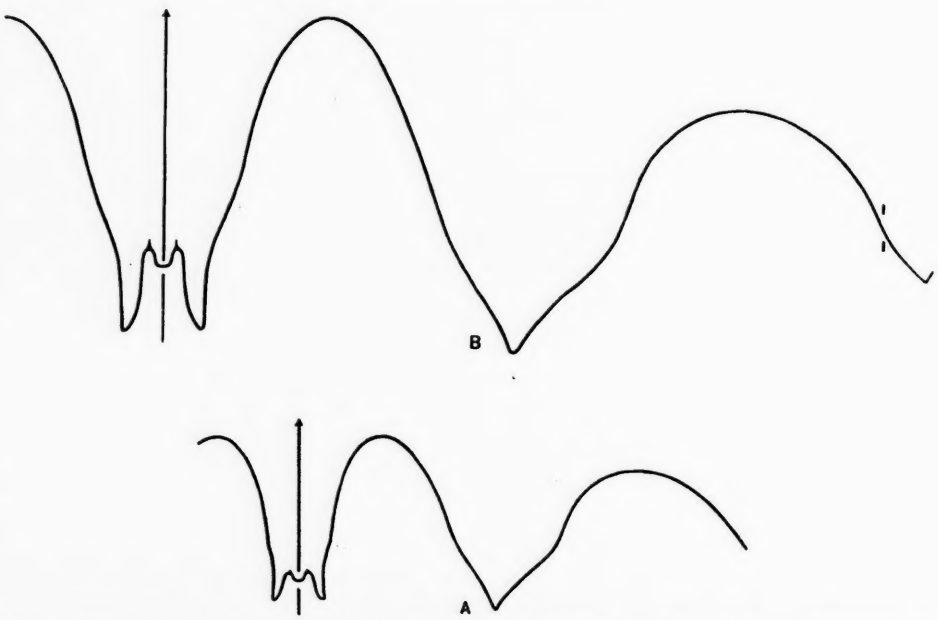
Discussion.—The Upper Peel River specimens appear to be similar in all respects to those described by Phillips and others in the type area, and, in turn, by Gordon in Alaska. This species is represented in the collection by four well preserved calcite



TEXT-FIG. 1—Index Map.

pseudomorphs with partial pyrite replacement. All but one of these shows a well preserved suture. Bisat (1924, p. 80) has suggested that this species should be described as a group, with a number of subspecies related to apparent variation in suture, size of umbilicus, and shell ornament. No attempt has been made to identify subspecies in this study, however, due to the lack of preservation of sufficient shell material on the specimens. According to Bisat (*Ibid.*, p. 80) minor differences in suites of *G. crenistria* from localities in Northern England, do not have stratigraphic significance over any considerable area. This species, occurring as it does in Northwestern Canada, would appear to indicate an age of lower Chester; approximately upper Viséan (V_{3c} sous-assise) of the European scale (Delépine and Demanet, 1956).

Localities.—These forms were apparently recovered from a dark silty limestone member of the Mississippian section on the north bank of Upper Peel River, approximately 8 miles downstream from the mouth of Hart River.



TEXT-FIG. 2—Sutures of *Goniatites crenistria* Phillips, ×3½, from Peel River. (Univ. Alberta Coll.) *A*, Immature specimen at a diameter of 17 mm. *B*, Larger individual at a diameter of 24 mm.

TABLE 1—DIMENSIONS AND PROPORTIONS OF PEEL RIVER *Goniatites* (in mm.)

	A	B	C	D
Diameter	24.	17.	18.	25.
Height	14.5	15.	9.5	15.
Width	18.5	14.	—	17.
Umbilicus	2.5	1.7	1.7	3.
U/D	0.12	0.10	0.09	0.12
W/D	0.76	0.82	—	0.68
W/H	1.26	1.10	—	1.12

Another Western Canadian specimen, examined through the courtesy of Peter Harker and the California Standard Company, may be referable to the same species, *G. crenistria*. It is a relatively small pyritized form recovered by A. E. Kliske from the Banff Formation in southwestern District of Mackenzie, N. W. T. This locality is on Liard River about 50 miles north of Fort Liard, 500 miles southwest of the goniatites on Peel River and over 100 miles from the prelecanitid specimen described below. The horizon north of Fort Liard is believed to be some 1000 feet below the top of the Mississippian. However, Sutherland (1958) has determined a Mississippian section in the same general locality to be only 1150 feet in total thickness, with the lower portion Kinderhookian in age. Considerable difference in stratigraphic interpretation is therefore apparent, for the *Goniatites* may be regarded as an index for late Mississippian.

A NEW PROLECANITID SPECIES FROM LIARD RIVER AREA, BRITISH COLUMBIA

During the autumn of 1953, a prolecanitid specimen was discovered in a well core, Calvan-Central Leduc, Toad River No. 1, at depth 4455 feet. This specimen was sent, at that time, to P. S. Warren, at the University of Alberta, and in turn to A. K. Miller at the State University of Iowa. It represents the genus *Prolecanites*, in the restricted sense. This fossil is generally regarded as an excellent index of Meramec or lower Chester age of the Mississippian, but has been previously described in North America from only two localities: the Upper Mississippi Valley and the Eastern Interior. Species based on specimens in the British Museum have a comparable age in Ireland and Northern England.

The specimen under study exists as a compressed internal mold in black shale. From the well-log description of Toad River No. 1, this shale member is thought to belong to the Banff Formation, which sup-

posedly occurs in this section from depth 3530 to 5270 feet. The writers are indebted to L. E. Workman, who kindly supplied particulars on this well. It may be noticed, with regard to the Mississippian in this particular area, that the Rundle Formation is considerably more argillaceous than is generally known in the type section, and that the Banff is considerably more calcareous. Such a relationship would tend to suggest an affinity of the Mississippian of this area with that of north central Yukon Territory, in the Peel River Basin. The Mississippian of this area is not divided into smaller stratigraphic units, such as formations, but its lithology is characterized by clastic limestone with abundant shale units. The fact that this particular shale unit, at depth 4455, contains *Prolecanites* indicates the shale to be of Upper rather than Lower Mississippian age. Therefore, either this particular shale unit is not properly a part of the Banff, or the Banff equivalent in this area is considerably younger than that of the type area. Laudon & Chronic's study (1947,1949) of the Mississippian on the surface near the Alaska Highway, immediately to the south of this area, seems to bear out such a conclusion. However, no exact correlation with their units may be made.

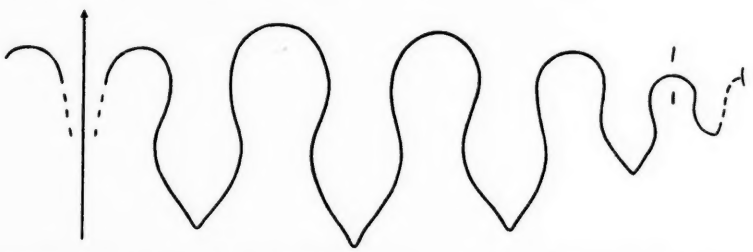
Genus PROLECANITES Mojsisovics, 1882
PROLECANITES WARRENI Sellers & Furnish, n. sp.
Pl. 141, fig. 6

The holotype of this species is from a well core and represents a volution of the phragmocone, plus parts of the body chamber. It is an internal mold which is slightly crushed and distorted but portrays diagnostic features.

The conch is discoidal, compressed and evolute. The whorls at diameter 53 mm. are higher than wide, but so flattened in the specimen under consideration that true dimension cannot be viewed. It has a diameter of 53 mm. probably up to 85 mm. including the body chamber. The height of the last whorl near adoral end is 22 mm., probably somewhat distorted. The form is widely umbilicate, nearly half the diameter. No trace of shell markings are visible on the specimen under study. The body chamber appears to occupy more than half a whorl.

Each mature suture consists of 14 lobes. The external suture as illustrated (Text-fig. 3) consists of an acuminate ventral lobe and five pointed linguiform lateral lobes on either side. Of these, the first three lateral lobes on the last whorl near the adoral end are of approximately equal dimension, with the second lateral lobe being the largest. The fourth and fifth lateral lobes, near the umbilical shoulder, are smaller than the others and markedly asymmetric. The nature of the internal suture could not be ascertained due to the nature of preservation in the specimen, but this feature is sufficiently constant within this genus to anticipate the outline.

Discussion.—The specimen under study appears to represent a species intermediate between *Prolecanites* and *Acrocanites*. A greater number of lobes exists on this individual than is typical of the former, and a lesser number of lobes than defined for the latter. Nevertheless, an apparent affinity may be demonstrated with three prolecanitid species described over a hundred years ago. These species are: *P. compressus* (Sowerby), *P. serpentinus* (Phillips) and *P. mixolobus* (Phillips). *P. warreni* would seem to be further advanced than these forms, as it exhibits one more completely developed lobe and saddle. Bisat has suggested that *P. mixolobus* and *P. serpentinus* are youthful forms, or forms closely allied in develop-



TEXT-FIG. 3—*Prolecanites warreni* Sellers & Furnish, n. sp. External suture of the holotype (Univ. Alberta Coll.); from well on Toad River at a depth of 4455 feet; diameter of 53 mm., ×6.

ment with *P. compressus*. This relationship may be illustrated by the similarity in the suture of the three forms, and the considerably greater size (diameter up to 160 mm.) of *P. compressus* than *P. serpentinus* and *P. mixolobus* (diameter about 20 mm.). The specimen under study does not coincide with either of these figures.

Apparent similarity may also be shown between the specimen under study and *Acrocanites multilobatus* Schindewolf. However, the latter form is considerably smaller (diameter about 27 mm.) and the suture, as illustrated, apparently consists of 18 to 20 lobes. This greater number would appear to place *A. multilobatus* as a more advanced form than *P. warreni*.

With regard to other known North American species, the specimen under study shows little affinity with *P. americanus* Miller & Garner or *P. monroensis* Worthen (Collinson, 1955) of the Ste. Genevieve Limestone of Indiana and Illinois, respectively. These latter forms show a 12-lobed suture which lacks the apparent regularity of *P. warreni*. These species also appear to be smaller, and to exhibit a more evenly rounded whorl than does the specimen under study.

The name of this species is in honor of Dr. P. S. Warren, Professor Emeritus of the University of Alberta, whose work in the field of stratigraphy and paleontology of Western Canada is recognized internationally.

Occurrence.—The specimen under study is preserved as a slightly compressed internal mold preserving fine detail. The matrix may be described as black silty fissile shale, apparently bituminous, noncalcareous and containing small pyrite nodules, and approximately horizontally bedded. It occurs in a well core, depth 4455 feet, Calvan-Central Leduc Toad River No. 1 (Map coordinates 94-N-7), British Columbia. This locality falls near the junction of the Toad and Liard Rivers.

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EXPLANATION OF PLATE 141

FIGS. *1–5—Goniatites crenistria* Phillips, ×2½. Three views of one specimen and two views of another (Univ. Alberta Coll.) from Upper Mississippian strata on Peel River, Yukon Territory.

6—Prolecanites warreni Sellers & Furnish, n. sp. ×2. View of slightly crushed holotype (Univ. Alberta Coll.) from well on Toad River, British Columbia, at a depth of 4455 feet. Upper right margin represents core-cut.

JOURNAL OF PALEONTOLOGY, V. 34, NO. 6, P. 1129–1152, PLS. 142, 143, 11 TEXT-FIGS., NOVEMBER, 1960

MONTECARIS LEHMANNI, A NEW CRUSTACEAN FROM THE RHENISH DEVONIAN AND THE PROBLEM OF ITS SYSTEMATIC POSITION

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ABSTRACT—A new phyllocarid, *Montecaris lehmanni*, has been found in the Devonian platy limestones of the Bergisch Gladbach syncline of the Rhenish Massif of Western Germany. This paper is presented in order to describe fully the fossil and its occurrence. After a discussion of the general profile of the area and the paleogeographic conditions in the middle and upper Devonian times, it is concluded that the Upper Plattenkalk resting above the lydite series belongs to the Frasnian group of strata because of diabase volcanism attendant upon its formation. The distribution of Upper Devonian rocks in this syncline is thus considerably enlarged.

Anatomic studies of the perfectly preserved specimen of *Montecaris lehmanni* Jux, n. sp., and comparison of it with related fossils and recent forms, reveal that the dorsal shield of phyllocarids correspond very closely to that of the Apodidae. Further, the development of the free abdominal region of *Montecaris lehmanni* is more related to that of the Apodidae than to the Nebaliacea, which is presently considered to be the group most related to fossil phyllocarids. The structure of the mandibles, found partly in fossil forms in their original locations, is much the same as that found in *Apus* and *Lepidurus*. The ventral appendages of *Nahecaris* and especially *Vachonisia* also show a clear correspondence to the Apodidae and with this evidence there can be no doubt that the fossil phyllocarids are an order of the Branchiopoda similar to Notostraca.

PREFACE

IN 1956 the author made initial announcements concerning the distribution of phyllocarid relicts in the Devonian rocks of the Bergisches Land of West Germany. These were based on fragments of carapaces which were not further described. These fragments were found in the dark bituminous, platy limestone transitional beds between the Givetian and Frasnian groups. Recently a new genus, *Montecaris*, was found in these beds and described by the author. The complete carapace and relicts of the abdomen, with its perfectly preserved telson, were both recorded. These fossils unfortunately were not in their natural contact.

Dr. T. Ørvig, of the Swedish Museum of Natural History, and Drs. Wo. Schmidt and M. Schürmann, both of the Geological Survey of Northrhine-Westfalia, Krefeld, undertook a systematic collection at the same site which brought, in addition to a rich assemblage of fish remains, new crustacean

EXPLANATION OF PLATE 142

FIG. *1*—*Montecaris lehmanni* Jux, n. sp. Holotypus, L. Upper Devonian (L. Frasnian), Bergisch Gladbach, Eulenberg, Rhenish Massif, W. Germany. *Collection:* Geol. Surv. Northrhine Westfalia (Krefeld), Inv. Nr. GiO 9a. (Detailed dimensions are given in the text.)

2—*Apus cancriformis*, Recent; length: 4.1 cm.

3—*Apus cancriformis*, having been artificially flattened in a book-press so as to demonstrate the deformation of the dorsal shield; observable are the same fracture systems as in *Montecaris lehmanni* Jux, n. sp. (refer to fig. 1).

material. This latter included a new species of *Montecaris* in which the carapace and abdomen were nearly completely preserved with their natural connection. This fossil will certainly shed new light on the still obscure systematic position of some of the phyllocarids.

The author wishes to express his sincere appreciation to Dr. Ørvig and Dr. Schmidt for their generosity in supplying this material on *Montecaris* for analysis.

The appointment was supported by the International Cooperation Administration under the Visiting Research Scientists Program administered by the National Academy of Sciences of the United States of America.

This paper is dedicated to the late Prof. W. M. Lehmann of the University of Bonn and it is hoped that it will in some small way acknowledge his endeavors in investigating the Lower Devonian fauna of the Hunsrück shales, which brought essential determinations for the understanding of Paleozoic fish, echinoderms, and arthropodes.

INTRODUCTION

The only phyllocarids previously described from the Devonian formations of the Bergisches Land were found in the Strunde stream valley near Bergisch Gladbach which is about 9 miles east of Cologne (Text-fig. 1). There they have been discovered in a quarry directly northeast of the Eulenburg tavern (Text-fig. 2). Fossils of this type also occur in quarries of nearby An der Loh and Heiligenstock. Schmidt discovered "teeth" of phyllocarids in the Upper Devonian Dorper Kalk near Elberfeld (Text-fig. 1); however, nothing was written about these remains. Klohn in 1928 mentioned relicts of phyllocarids in the black shales of Niederhemer which were stratigraphically the transitional beds between the Upper Devonian and Lower Carboniferous. These rocks, however, in their facial aspects, very much resemble the beds that include corresponding fossils near Bergisch Gladbach.

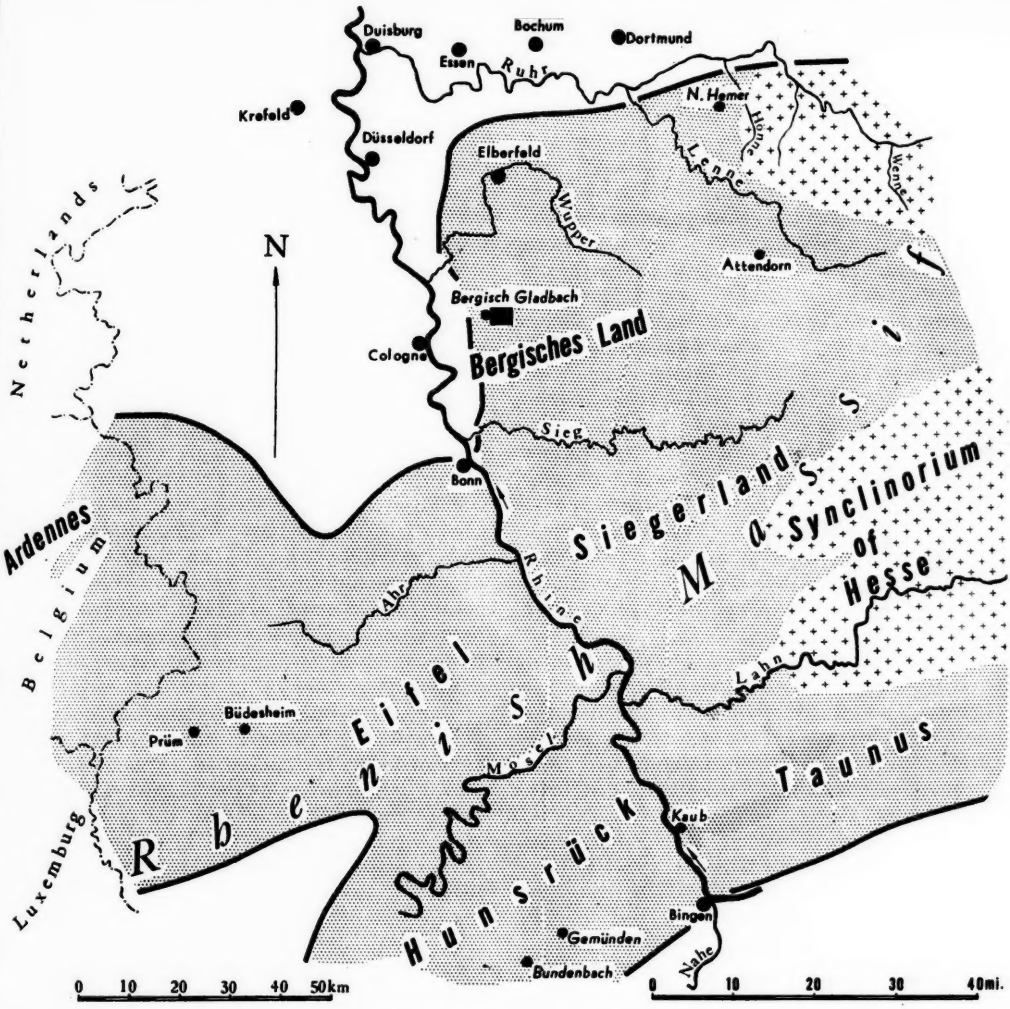
Poorly preserved species, whose identification was based solely upon telsons, were made known by Ludwig in 1863–64. These were the *Dithyrocaris kochi* of the Upper Devonian limestones of the Hesse synclinorium and the *Dithyrocaris breviaculeatus* of the sandy Lower Devonian from the same region.

In the Rhenish Massif well preserved phyllocarids had been previously observed by Broili (1928/30), Hennig (1919/21) and Jaeckel in the Lower Devonian Hunsrück shales at Bundenbach, Gemünden and Kaub (Text-fig. 1). Some of the fossils observed displayed large fragments of carapaces and abdomens in their natural connection. By far the most numerous descriptions of phyllocarids have been obtained from American and British discovery sites.

Phyllocarids are commonly found in the facies of fine-grained pelitic basin deposits and are often fossilized together with tentaculites, styliolines, conularians, cephalopods, and fish remains. Beds such as these are poor in benthonic fossils. Ruedemann in 1934 presented clear pictures of the lithological and biofacial conditions of American rock in which the phyllocarids occur along with Paleozoic plankton.

The general situation is very similar at Bergisch Gladbach. The Middle and Upper Devonian strata form a syncline there which is well known because of its rich fossil content. The beds exposed in the valley of the Strunde are a monotonous sequence of thin bedded dark limestones, that split into still thinner even layers when weathered. This rock is usually extremely poor in fossils.

These beds reach a thickness of several hundred feet in the valley of the Strunde. The rock below is a massive limestone locally named Massenkalk in which are found stromatopores, *Amphipora ramosa* Phill., *Disphyllum caespitosum* (Gf.), *Stringocephalus burtini* Defr., *Uncites gryphus* Schl. along with numerous other species of the rich Givetian fauna that lived in the surroundings of large biostromes. The rock overlying the previously mentioned platy limestones are shales and clays which include species such as *Manticoceras intumescens* Sandb., *Tentaculites tenuicinctus* Roem. and *Styliolina laevis* R. This is a series of beds that can be correlated and easily compared to the Matagne shales of Belgium



TEXT-FIG. *1*—Northwestern Germany (Rhenish Massif) with localities mentioned in the text. Dotted area near Bergisch Gladbach represented by the geologic map on Text-figure 2.

which have their equivalents in the Eifel as in the shales of Büdesheim (syncline of Prüm).

The Matagne shales are significant for the Upper Frasnian (=Upper Adorf). They overlap the Upper Devonian shales of Fromelennes and Frasne in Belgium and in the Eifel the dolomites of Wallersheim as well as platy limestones of Oos. Therefore a great deal of the platy limestones of the Bergisch Gladbach syncline should be considered a part of the Frasnian.

In spite of the monotonous lithological character of these platy limestones, which is plainly seen in all outcrops, their subdivision into four series is feasible. In the middle part of the profile, flinty layers appear together with bands of chert geodes. This peculiar facies brings out the direct connection with the diabase volcanism that

gave origin to great amounts of tuffites in the eastern Rhenish Massif and in the synclinorium of Hesse at the Middle-Upper Devonian boundary.

The diabase tuffites in the valley of the Hönne and in the east of Attendorn (Text-fig. 1) in the Wenne district, near Bergisch Gladbach, overlie and interfinger with the limestones of Givetian age which have been identified by fossils. The platy limestones of the Bergisch Gladbach syncline below the lydite series (Text-fig. 2) should be shown as belonging to the higher Givetian (=Lower Plattenkalk). Thus the overlying Upper Plattenkalk is part of the Upper Devonian. This is especially notable in the reef limestone series which is characterized by the thinly developed coral and stromatopore reefs, reflecting a lithological as well as a biological change in the facies. The rich fauna found in these rocks, in particular the tabulate corals (*Thamnopora, Alveolites* etc.) have a significant Upper Devonian character.

In the reef limestone series the influence of a distant submarine volcanic activity is clearly noted by chert layers containing remarkable trace elements. Here, too, the relation to an Upper Devonian diabase volcanism in the previously mentioned areas is obvious.

It is mentioned that M. Lecompte attributed the magnificent reefs in the Frasnian of the Ardennes (Text-fig. 1) to epeirogenetic movements: uplifts and subsidences. It seems evident that these oscillations are marked in the Rhenish geosyncline leading up to the volcanic districts in its eastern parts.

What can be said about the fossil content in the Upper and Lower Plattenkalk, separated from each other by the lydite series (Text-fig. 2)? The stromatopore biostromes of the Givetian Massenkalk gradually pass over in its upper parts, and also along its flanks, into well bedded detrital limestones, indicating the talus of the big reefs. For this reason a rich fauna is to be observed in the Lower Plattenkalk as it interfingers the Massenkalk and may replace it completely, as is the case with the Flinz shales in parts of the northeastern Rhenish Massif.

The fauna of Lower Plattenkalk is characterized by brachiopods. *Stringocephalus* appears sporadically. In the main, however, it is replaced by *S. dorsalis* Gf., appearing together with *Newberria caiqua* A.V., *Denckmannia damesi* Hzl. and especially *Spirifer hians* V.B. and *Sp.* (*Martinia*) *inflatus* Schn. Besides these fossils planktonic and nektonic varieties appear commonly. These are several species of tentaculites and goniatites, among them the Givetian guide fossil *Maeneceras terebratum* Sdbg.

There is no doubt as to the Givetian age of this series, but the fauna of the Upper Plattenkalk appears very different. Benthonic fossils are represented only by a few small, smooth spiriferids (*Sp.* (*Martinia*) *inflatus* Schn. and *Sp. hians* V.B.), occasionally *Gypidula, Athyris* and *Atrypa*. Sometimes the surface of layers may be heavily covered with *Lingula subparallela* Sdbg. Only in some of the thicker beds of compact limestones, fragments of branched corals (*Disphyllum*) and Hydrozoa (*Amphipora*) appear. The biofacies is characterized by tentaculites, styliolines and very often by floated remains of psilophytes.

The strata cropping out near Eulenburg belong to the Upper Plattenkalk, where a typical facies is exposed in a quarry. Here and in the quarries of the surrounding area the phyllocarids which are the subject of this paper were collected. They occur together with fish remains, sometimes perfectly preserved, and have been studied by Ørvig and Schmidt.

Gross in 1938 and 1953 described the arthrodire *Rachiosteus pterygiatus* from the platy limestones of the Strunde valley and the minute palaeoniscide *Moythomasia nitida* from the Heiligenstock quarry. The following fish remains have been tentatively identified by Ørvig in his unpublished study: *Atopacanthus* sp., *Rachiosteus pterygiatus* Gr., *Ptyctodus* sp., *Chelophorus?* sp., *Antiarchi?* gen. et sp. indet., *Ganorhynchus?* sp., *Dipterus* sp., *Rhinodipterus?* sp., *Ostiolepiformes, Gluptolepis* sp., *Diplocercides?* sp., *Moythomasia nitida* Gr.

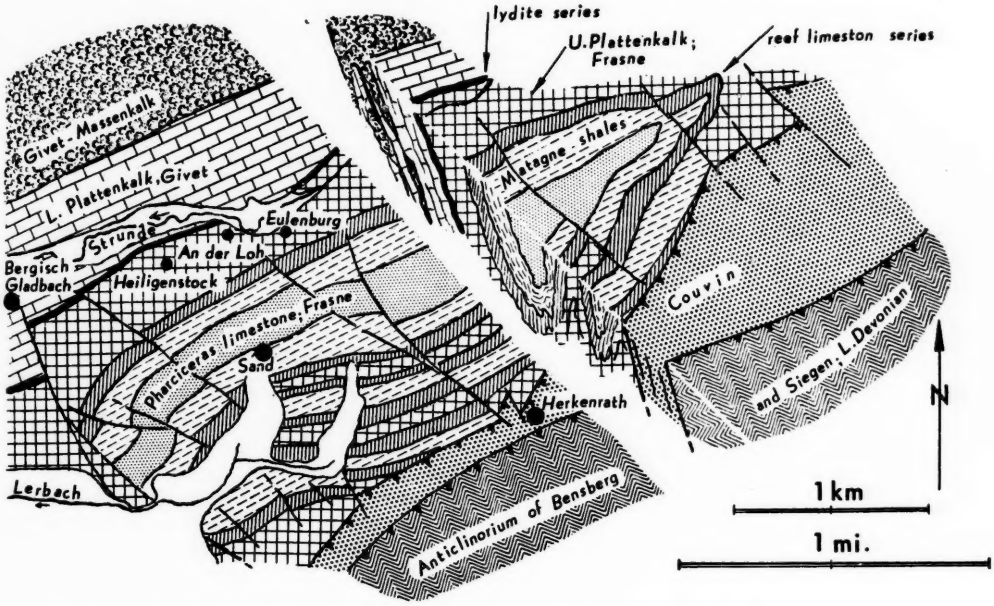
The Upper Plattenkalk is considered a basin deposit far off the coast. Sedimentation was below a depth in which stromatopores and corals found favorable conditions. The Upper Plattenkalk therefore proves a regional subsidence, causing the

mighty biostromes to cease and spread over a region north of the area where platy limestones were deposited. In Text-figure 2 some of the facial, paleogeographic and tectonic relations of the district are to be seen. The Couvinian, forming the border of the syncline, is represented in its higher stages by sandstones, greywackes and shales (= Honseler beds). The biostromes which built up the Massenkalk developed out of small *Hexagonaria* bioherms. The basin to the south of the Massenkalk biostromes were the main regions in which platy limestones and shales were deposited. Because of strong subsidence they reach great thickness, obtaining their fine detrital material chiefly from the area covered by biostromes, continuing with widely extending stromatopore carpets farther into the zone of turbulent waters.

The diabase volcanism beginning in the highest Givetian and lowermost Frasnian indicates a stronger subsidence in the geosyncline and thus it is linked with the regional encroachment of the deeper basin facies. Positive epeirogenetic movements are not noted before the formation of the reef limestone series in middle Frasnian time, yet this incident is immediately followed by a new regional subsidence, which is reflected by the *Buchiola* shales of the Matagne facies (Text-fig. 2).

The epeirogenetic development of this region has been previously discussed in detail; however, this short summary may indicate that the beds in which phyllocarids occur in the Strunde valley are characterized as a basin facies with poor benthonic fauna. It is a marine facies, as reflected by the presence of brachiopods, goniatites and sporadic coral fragments. The significance of recently discovered fish remains is emphasized as they concern species which up to now were thought to be of the Old Red. Similar problems must be dealt with in discussing the systematic position of the phyllocarid remains.

It is remarkable that corresponding relicts, unfortunately only fragments, have been found in the black shales of Niederhemer, where, to quote Klohn, a similar bathymetric situation was found which is not different from that in the Hunsrück



TEXT-FIG. 2—Geologic map and cross-section through the central part of Bergisch Gladbach syncline. Localities pointed are mentioned in the text.

shales. Deeper water conditions as proved by fossil content and lithofacies will only indicate in a sense that the fortunate situation for reef formation was no longer present and that directly observable terrigenous influences were largely pushed back. A continental region seems to be indicated by the psilophytes but they have not been studied in detail. Because they may float over great distances they may offer no reference to the actual paleogeography. Finally, the fossil findings from the synclinorium of Hesse (Ludwig 1863/64) and from the Upper Devonian limestones near Elberfeld point out that phyllocarids may have lived in the reef areas as well as in the surrounding shore facies.

The floor of the Plattenkalk basin was not at all inimical to life and it is possible to demonstrate very similar sedimentological structures, for example, the Hunsrück shales which R. Richter described in 1931. This is a proof for good ventilation of the strata next to the sea floor and currents in water as evidenced by ripple marks and cross-bedding even in the pelitic layers.

The poor content in benthonic fossils, however, is not to be explained here by selective documentation (pyritization, etc.); yet it may be related to the question of the food situation for the bottom living fauna.

NEW MATERIAL

Among the new material obtained from Stockholm and now in the collection of the Geological Survey of Northrhine Westfalia are some uniform limestone plates of dark color containing phyllocarid remains on their surface. One of them appears as a large crushed carapace, which is easily identified as *Montecaris*. The destruction of the preservable parts of the fossil took place before the process of fossilization could be completed and currents are responsible for the arrangement as it is found today.

Another plate contains a phyllocarid in which abdomen and valve are preserved in their natural connection. Its counterpart is also preserved, and it has fixed in its anterior part important fragments of the carapace, while on its posterior relicts of abdominal rings remain.

Carapace and abdomen are planed to the surface of the layer on a dark grey, fine-grained platy limestone that may be defoliated in minute strata because of its extremely thin even bedding. Both valve and abdomen permit study of finer structures of the sculpture. Dorsal shield and abdominal somites show only little fracturing which can be explained by the flattening due to sedimentary load.

Between carapace and abdomen a "Psilophyton" obscures the articulation of the first abdominal rings. Yet all three of them are in their firm connection. The same specimen shows the telson with its powerful main spine, armed with bristles, and both of the longer, flame shaped cercopodes.

This fossil, exhibiting all the characteristic features of the genus *Montecaris* Jux, allows a detailed knowledge of carapace and abdomen, until now observed only from isolated valves and telsons.

There are remarkable differences in the newly found fossil, separating it from *Montecaris strunensis* Jux. It is larger, more stumpy, with stronger sculpturing and in parts, for example in the telson, different from known species. These may be a sexual differentiation, as is found in the Leptostraca of today being compared too readily with the phyllocarids. This is difficult or even impossible to control in the extremely rarely occurring complete fossil specimens. It should be borne in mind that most of the species by far were identified only on the basis of telsons or valves. Therefore a new species name should be introduced.

DESCRIPTION

Genus MONTECARIS Jux 1959

MONTECARIS LEHMANNI Jux, n. sp.

Text-fig. 3A; Pl. 142, fig. 1, Pl. 143, fig. 1

Type species: *Montecaris strunensis* Jux

Derivatio nominis.—Dedicated to Prof. W. M. Lehmann (University of Bonn). His palaeontological researches in the Hunsrück shales, especially the discovery and detailed description of *Vachonisia rogeri*, proved to be a substantial aid in interpreting the systematic position of the new species and the phyllocarids.

Typus.—The phyllocarid with complete valve and abdomen represented on Plate 142, fig. 7 and Text-figure 3A; collection of

the Geol. Survey of Northrhine Westfalia, W.-Germany, Inv. Nr. GiO 9a.

Cotypus.—The counterpart of the same phyllocarid displayed on Plate. 143, figure 1. Collection Geol. Surv. Northrhine Westfalia, Inv. Nr. GiO 9b.

Locus typicus.—Large quarry at Eulenburg near Bergisch Gladbach, Rhenish Massif, W.-Germany. Coordinates: Topog. map 1: 25,000, sheet Mülheim/Rhine, r=8172, h=5180.

Stratum typicum.—Upper Plattenkalk near the border Givetian/Frasnian; most probably lowermost Frasnian.

Diagnosis.—A species of *Montecaris:* With a horseshoe-shaped valve, straight dorsal rim, an anterior dorsal furrow and in front of it a row of three elevated nodes, both lateral halves of the flattened valve nearly egg shaped with a broader circulating marginal border running out in stumpy posterolateral and posterodorsal spines.

With an abdomen having three visible smooth somites overlapping each other posteriorly with lateral spines.

With a vigorous dagger-shaped telson spine bordered by stronger bristles, being flanked by two longer and smooth flame-shaped marginal spines.

DEFINITION OF THE GENUS AND PREVIOUSLY DESCRIBED MATERIAL

The genus *Montecaris* has been defined on the basis of fossils found at the quarry "An der Eulenburg" (Jux 1959). These fossils consisted of a complete carapace and a telson with relicts of both of its last abdominal rings. The definition of the genus emphasizes the two nearly egg-shaped valves of the carapace connected by a straight dorsal border; a vigorous central spine of the telson flanked on both marginal rims with strong, saw-shaped bristles, and a shorter stumpy central spine compared with the broad flamelike marginal spines.

The carapace of *Montecaris strunensis* reaches a dorsal length of 50 mm. and a maximum width of 35–38 mm. Both the valve halves are separated marginally by a shallow dorsal rim, while the surface of the valve is generally smooth or only slightly scarred. A rim also occurs on both sides of the lateral valve. Bulges and furrowlike depressions on the dorsal region are observed which trend from the median suture ventrally and end in the middle field. The new findings show that these significant dorsal depressions had been situated in the animal's anterior, since the egg-shaped shield halves taper anteriorly, not posteriorly (Jux 1959). The posterolateral regions in both species are characterized by a spiny process similar to *Mesothyra oceani* Hall & Clarke which consequently makes the orientation of the carapace relatively simple.

The telson of the genotype has a 28 mm. long central spine, the maximum width of which is 6 mm. The length of the lateral spines reaches 35 mm. Both central and marginal spines are keeled and smooth but have a fine longitudinal striation. The central spine is set with markedly saw-shaped bristles pointing posteriorly.

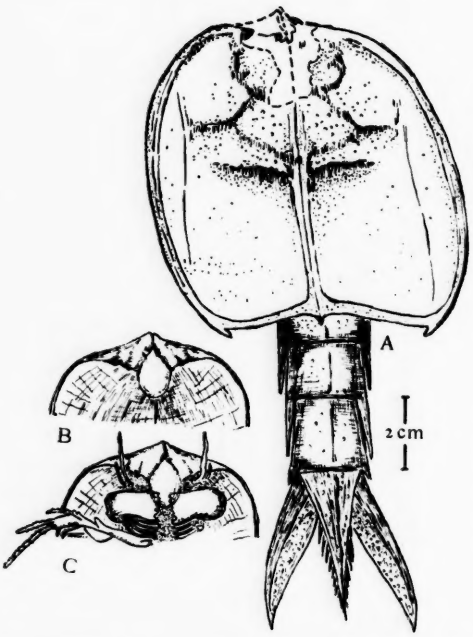
The mode of preservation of the *Montecaris strunensis* remains mentioned corresponds generally to the new material (cf. Jux 1959).

CARAPACE OF THE NEW FINDINGS

On the flat valve the demarcation between the two long oval carapace halves that widen in the posterior part is represented by a straight median line (Text-fig. 3; Pl. 142, fig. 1). As is generally the case in phyllocarids, a hinge mechanism is not present and in study of this region under the binocular microscope it is to be noted that both halves of the valve join each other without a break along a ridge. The only differentiation is an unequal thickness of the plating.

For this reason, isolated yet complete dorsal shields are found relatively often. Had there been a fixation due only to muscles fixing both halves along a hinge line, as is often stated, the reverse observation would be the rule.

Montecaris had a connected uniform dorsal shield that was clearly divided in two lateral regions. Possibly the median suture was of importance in the process of casting the skin or it may also be that a certain movement of both shield halves against each other was possible. This seems obvious, as both the egg-shaped valve halves taper anteriorly and touch each other with two horny spurs at the median suture which in the present fossil are gaping.



TEXT-FIG. 3—*Montecaris lehmanni* Jux, n. sp. and the reconstruction of its ventral anterior part (BC).

On the posterior part of the shield the connecting median suture terminates in a spiny process. Both the carapace halves show a concave-convex curved marginal rim at this point ending in two prominent posterolateral spines, which are also significant in *M. strunensis*. The ventral border line continues in a regular half oval and is ornamented with a constant bulge line (Text-fig. 3; Pl. 142, fig. 1) embracing both shield sides in its anterior and posterior portion.

The dorsal shield exhibits, on both its ventral fields, longitudinal stripes which resemble secants; such structures are observed in *M. strunensis* as well as in many other phyllocarids (for example, *Nahecaris*, *Mesothyra*, *Ceratiocaris*, *Caryocaris*, *Ptychocaris*, *Tropidocaris*). In *Montecaris* and in many of the forms mentioned, these are secondary structures originated in the flattening of the dishlike dorsal shield. This is a hint that the carapace of *Montecaris* closely resembles the general form of *Galenocaris campbelli*, described by Wells (1944).

SCULPTURING

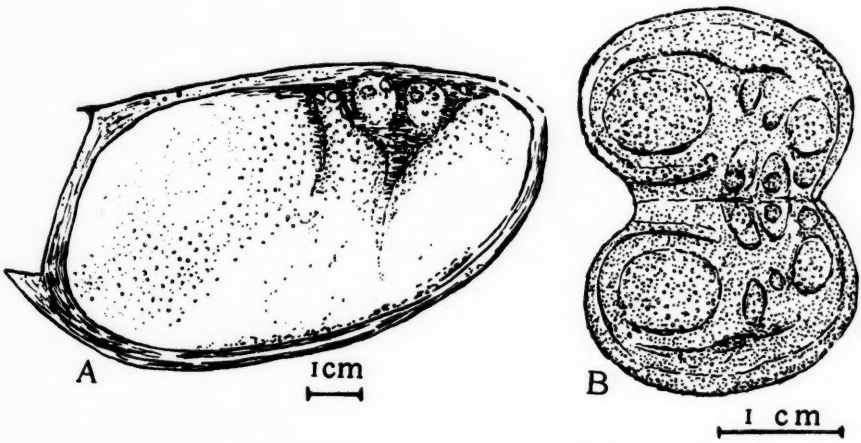
M. lehmanni displays in the anterior valve region characteristic furrows and bulges which are significant for many phyllocarids. A broad groove, inclining a bit anteriorly, extends from the dorsal median ridge in a ventral direction. The groove smooths out gradually in the middle fields of the valve halves (Text-fig. 3). In front of this depression and, separated from it by an oblong hump, there stretches a second furrow connecting, with a regularly ordered groove, regions of the most anterior dorsal shield.

In the extent of this sculpture, the carapace appears to have characteristic scars consisting of small crater-shaped structures associated with warty features (Text-fig. 3; Pl. 142, fig. 1). This is a remarkable contrast when compared with the much smoother sculpture of the posterior part and the ventral lobes.

FRONTAL REGION

It has been already mentioned that both halves of the dorsal shield run out in the anterior dorsal part in two horny tips and that the valve there curves off in a ventral direction. A gap then breaks the continuity of the median suture. It is in this region that a "rostrum" was often found and credited with being the chief evidence for a systematic connection of phyllocarids with modern Nebaliacea. *M. lehmanni* does not appear to show such structures. In the region of the so-called "rostrum" a large piece of the fossil broke off when splitting the limestone plate in order to expose the specimen. This turned out to be a fortunate accident, for the missing fossil fragment remained fixed on the counterpart and thus the original exhibits deeper structures otherwise obscured.

A row of ventrally slanted and folded minute plates are present on the specimen and it is easy to see their original relationship to the upper anterior valve part which gives proof that *Montecaris* possessed a shield that bent down and backward in the frontal region. It is most probable that a subfrontal plate filled part of the space between the anterior valve part and the enlarging median gap. Text-figure 3B indicates the most probable reconstruction of this region.



TEXT-FIG. 4—*A*, *Montecaris strunensis* Jux (right half of the dorsal shield). *B*, *Echinocaris crosbyensis* Eller (Carapace after Eller 1935).

COMPARISON WITH THE DORSAL SHIELD OF *MONTECARIS STRUNENSIS*

The carapace of *M. strunensis* was described with both its plates in their natural connection in a similar state of preservation as in *M. lehmanni*, n. sp. Yet isolated valve halves of this species have been found. Text-figure 4 shows such a specimen, which was collected in the quarry at "An der Loh" (Text-fig. 2).

This half valve (now in the collection of L.S.U. Geol. Dept., Baton Rouge) clearly shows the missing hinge line. Any form of articulation mechanism is lacking and the left part of the dorsal shield has been torn off the one represented here. The preserved right part was also broken on the ventral margin when plated by the load of sediments. The specimen is a bit larger than the genotype although it corresponds to it completely with respect to sculpture and ornamentation. The scarring is much finer than that observed on *M. lehmanni* and generally the warty tubercles are missing. Thus they are mentioned only in the region of three bulges in the anterior part near the median line which are separated by depressions trending similarly to those in *M. lehmanni* in a ventral and frontal direction (Text-fig. 4).

Corresponding to the new species is the general shape of this shield half, the marginal bulge line, and the spiny processes in their posterolateral and dorsal positions.

ABDOMEN

The abdomen, with its free abdominal rings and telson, projects below the posterior dorsal shield. The segments have the form of smooth chitinous rings that produce long spines laterally where each ring slighlty overlaps its successor. These long spines extend over half of the following somite and only in the most posterior abdominal ring are these spines shorter and more blunt (Text-fig. 3). The surfaces of these rings, that actually allow only movements in a ventral and dorsal direction, are slightly channeled in a longitudinal direction; occasionally irregular warty tubercles may be seen on them. Dorsally the valve keel can be traced backward over the different somites to the telson spine.

The main spine is significant for the genus in that it appears to be a bit shorter than the flame-shaped lateral spines and it projects straight back with a dagger shape and a prominent keel. Its surface also indicates a longitudinal channeling with warty tubercles. Strong bristles typically fringe both the margins.

The articulation of the lateral spines with the single final abdominal ring, which is longer than the one afront, is covered by the base of the central spine. The lateral

TABLE 1—DIMENSIONS OF THE DORSAL SHIELD OF *Montecaris* Jux

Measurements	*M. strunensis*		*M. lehmanni*
	Type specimen	Baton Rouge specimen	
Length of the carapace on its dorsal rim	50 mm.	70 mm.	92 mm.
Width of the shield halves at and parallel to the posterior dorsal furrow	33 mm.	50 mm.	52 mm.
Maximum length of the shield halves (parallel to the median line)	62–64 mm.	88–90 mm.	195 mm.
Distance between posterior dorsal and ventral spines	28 mm.	33 mm.	58 mm.
Distance between posterodorsal spine and posterior furrow	32 mm.	37 mm.	44–46 mm.

spines have a smooth surface along the external borders while the interior part is slightly scarred.

COMPARISON WITH THE ABDOMEN OF *MONTECARIS STRUNENSIS*

The state of preservation of the abdominal rings of *M. strunensis* is insufficient for a comparison with *M. lehmanni*. Nevertheless lateral spiny processes of the latter with one segment are also present, thereby distinctly proving that only a similar restricted movement was possible. It may be mentioned that the connection of the somites is principally the same as between the valve halves in which each segment is bound to the other by a narrow area, the chitinization of that articulate membrane being less pronounced than that of the segments themselves. It is no wonder, therefore, that Hall & Clarke (1888) could not present a clear picture when discussing the mechanism of a possible articulation between the carapace halves of *Mesothyra*. The fragment of a dorsal shield described in this paper indicates clearly the mode of connection in that particular instance as well as in others.

The telson of *M. strunensis*, again, is very similar to that of *M. lehmanni*. The lateral spines are, however, relatively much longer and more elegantly curved. They possess a significant median keel and are completely smooth; still the flamelike shape remains. In the last analysis, the central spine indicates the greatest correspondence. In *M. strunensis* it is stumpy, straight, resembling a dagger, has a prominent median keel and is especially characterized by its marginal bristles. These bristles are more pronounced in the new species.

There is little to be said concerning the articulation of the lateral spines in *M. strunensis* or *M. lehmanni* as represented only by their dorsal surfaces.

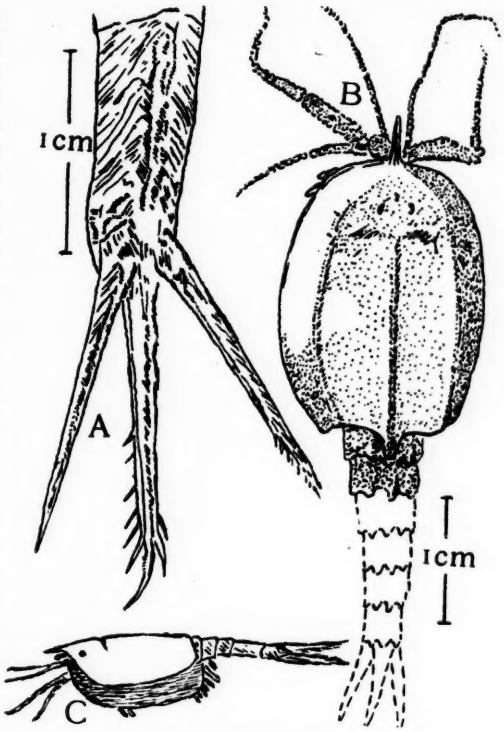
MONTECARIS LEHMANNI COMPARED WITH RELATED FORMS

In searching for phyllocarids related to *Montecaris* it appears logical to outline first the documentation in the Rhenish Massif. There is not much to say considering its region east to the Rhine, for the statements of Klohn (1928) are of as little aid as Schmidt's reference concerning the occurrence of phyllocarid "teeth" in the limestones of Dorp near Elberfeld (Text-fig. 1). The phyllocarid species established by Ludwig (1863/64) are not definitely applied to *Dithyrocaris* Scouler (Gürich 1929) although they may be very similar to certain species of *Ceratiocaris* or to *Mesothyra neptuni* Hall & Clarke. They are totally different from *Montecaris* as regards sculpturing and shape of spines. In addition the central spine does not contain the significant bristles.

Analogies are seen in some Lower Devonian species found in the Hunsrück shales (Text-fig. 1). Broili (1930) describes *Nahe-*

caris balssi from Bundenbach which, in spite of badly represented relicts of the dorsal shield and some of its appendages, permits an examination of the perfectly preserved telson. In this species the telson develops from a long penultimate abdominal ring and the lance-shaped lateral spines are slightly longer than the central spine. The central spine has a lance shape and contains on both its margins large vigorous prickles at the posterior part, while the lateral spines have only very fine rows of setae (Text-fig. 5A). This identifies the characteristics of Broili's species, and in his opinion it could be taken as the basis of a new genus. However, in the *Nahecaris* possible sexual differentiations should not be disregarded since the abdominal regions of the described *Nahecaris stuertzi* Jaeckel are not too well known.

What is the case in the development of the dorsal shields in *Nahecaris?* The new species described by Broili does not allow much discussion, since he is not certain of the identification of a thorn-shaped prolongation of the dorsal anterior rim as a "rostrum." Broili and Hennig (1922) discovered both, contrary to the findings of Gürich (1929), who recommended a bipartite carapace, as a uniform dorsal shield in their material of *Nahecaris*. In the anterior part there is no movable rostrum; thus *Nahecaris* has a dorsal shield like a dish with



TEXT-FIG. 5—*Nahecaris* Jaeckel 1921, Lower Devonian, Hunsrück. *A*, Telson of *N. balssi* Broili. *B*, *N. stuertzi* Jaeckel (after Jaeckel 1921). *C*, Reconstruction of *N. stuertzi* (after Broili (1929).

TABLE 2—COMPARISON OF ABDOMINAL SEGMENTS OF *Montecaris lehmanni* AND *M. strunensis*

Measurements (mm.)	*M. lehmanni*	*M. strunensis*
Length of the free abdomen (between posterior dorsal spine of the valve and the end of the central spine of the telson)	99 mm.	?
Abdominal rings:		
a) penultimate. Diameter at anterior articulation membrane	24 mm.	?
median length	18 mm.	?
length of marginal spine	18 mm.	?
basal diameter of marginal spine	3 mm.	?
b) ultimate. Diameter at anterior articulation membrane	18 mm.	7 mm.?
median length	20 mm.	4 mm.?
Telson:		
a) central spine. Median length	50 mm.	28 mm.
basal diameter	17 mm.	6 mm.
length of marginal bristles	6–9 mm.	2 mm.
basal diameter of marginal bristles	1 mm.	0.5 mm.
b) lateral spines. Maximum length	52–53 mm.	35 mm.
maximum diameter	12 mm.	6–7 mm.

a dorsal median ledge and two marginal ledges, with an anterior dorsal and thorny projection and also posterolateral spines, that do no appear clearly in the reconstructions published. This and the development of the abdominal region are surely marks that resemble the general organization of *Montecaris* (Text-fig. 5ABC).

Hennig pointed out that *Dithyrocaris* is more closely related to the nahecarids than all the phyllocarids. Jones & Woodward (1898) described abundant material found in the Carboniferous of Scotland. The carapace resembles very much the one of *Montecaris*. Many specimens show clearly the primarily uniform valve and it is odd that in the region of highest stress when flattening of the body occurs the gap thus originated between the torn median suture and the carapace is often filled in during reconstructions by hypothetical rostrums (as in Hall & Clarke), yet the preservation of these specimens is very different. The deformation due to the sedimentary pressures is very clearly observed in *Dithyrocaris granulata* W. & E. (Jones & Woodward 1898, pl. XX, fig. 3ab) where it is easy to return the specimen to its initial shape and in *D. testudinea* Scouler (pl. XIX, fig. 7) the original structure is completely evident.

Contrary to *Montecaris* the dorsal shields in the Dithyrocaridae extend farther; yet the general shape, the anterior dorsal peak and the posterior lateral spines are very much the same. Only sculpture and the development of the telson, both resembling *Montecaris*, are the deviations.

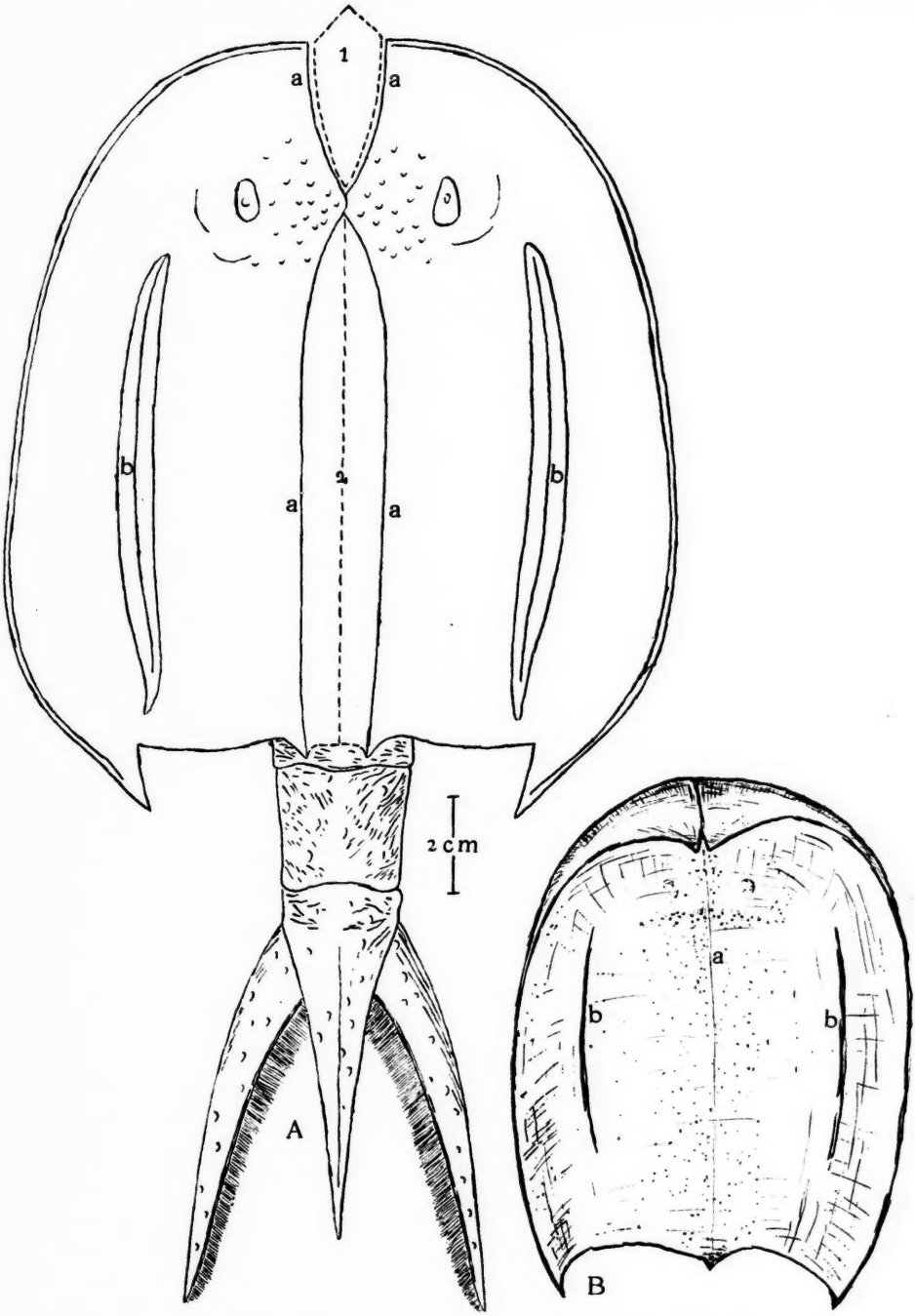
A model specimen of a movable rostrum in between lateral movable shields of a bipartite valve is *Mesothyra oceani* Hall & Clarke. This fossil found in the Upper North American Middle Devonian, first compared to *Dithyrocaris* (Hennig 1922), seems to possess a carapace that is similar to those already mentioned. The abdomen is somewhat similar to *Montecaris* (Text-fig. 6A) in that two abdominal rings and a stumpy, dagger-shaped telson protrude behind the carapace. The central spine is flanked by two flamelike cercopods with setaceous fimbriae along their interior margin.

The well known reconstruction of *Mesothyra oceani* was done from isolated fragments and must be considered in that light. Examination of the separated fossil pieces of the carapace that are the basis of Hall & Clarke's reconstruction, strong compression and strain tears are detected as they appear when a hollow convex body is flattened. However, the fossil material thus formed produced no relicts of a rostrum or fragments of a dorsal plate; these were introduced entirely by conjecture. These invented pieces do of course fill the gaps in the dorsal and anterior parts along the median line of the fossil; however, in the uncompressed valve body these plates are neglected. Hennig (1922) made some critical remarks concerning this reconstruction but they have not hindered its survival, since it is still to be found in the *Traité de Paléontologie*.

There is a simple way of reconstructing the original valve shape of *Mesothyra*, when both outlines of the available half of the carapace are traced on paper, cut out, and are joined together along the median suture. By doing this a uniform, broad horseshoe-shaped valve (Text-fig. 6B) developes which bends inward along the frontal region.

Actually paleontologists found among Ceratiocaridae chitinous plates, which were observed near the anterior dorsal end of the valve and are identified as "rostrum." These plates link the phyllocarids to the living Nebaliacea. The best example in this respect is *Ceratiocaris papilio* Salter, an often mentioned phyllocarid from the Ordovician of Britain. Good representations of this are to be found in Jones & Woodward (1888, pl. XII).

These "rostral" structures of Ceratiocaridae mentioned in the literature were nearly always found and pictured in lateral position, thus these fossils are compressed. The "rostrum" has its place normally a bit in front of the dorsal peak of the carapace. In view of the kind of rostrum seen today in *Nebalia* (Text-fig. 7), this type of embedding appears plausible. But now the question of the antennae arises, since after all these should also be preserved. The dorsal rim of *Ceratiocaris* is bent down anteriorly, much more than is the case with *Nebalia;* furthermore the whole frontal carapace is formed in such a way that it has a shape very similar to the valve of *Lepidurus* which



TEXT-FIG. 6—*A*, Hypothetic reconstruction of *Mesothyra oceani* Hall & Clarke. *B*, Valve reconstruction of *M. oceani* after omitting all invented plates.

is restored to the unflattened dishlike body. Considering this, there is in the dorsal frontal part no anatomically logical place for a "rostrum." This so-called chitinous plate therefore should have been placed at a different position than it is in *Nebalia* and therefore the term "rostrum" must be abolished.

LIVING SPACE OF *MONTECARIS*

The phyllocarid remains from the platy limestones of Bergisch Gladbach became fossilized in a pure marine facies. This is proven by their common occurrence with Brachiopoda (*Lingula*, *Atrypa*, *Athyris*, *Gypidula* and small Spiriferidae) and lamellibranchiates (*Aviculopecten*), which indicate a benthos lacking in species. The marine environment is further shown by the proximity of coral and stromatopore reefs.

A post-mortal drift to another area must not be overlooked. Tentaculities and styliolines occasionally concentrated on the surfaces of several beds sometimes clearly show the activities of currents. Psilophytes very often support the conclusion of movement of masses of continental organisms. These forerunners of continental vegetation are mostly not found in the small sized chaff which is generally present; instead they appear normally in longer stems which sometimes reach half a meter, with a diameter of only 1 cm. It may be that these psilophytes are really algae; this can not be conclusively stated until they are carefully studied.

Phyllocarid relicts could have drifted in from a different living space, perhaps even from a continental area. This idea is not based only on the psilophyte remains but it finds a special support in the fish relicts collected and to be discussed by Ørvig & Schmidt. Finally among them there appear specimens that are characteristic in the Old Red and therefore completely unexpected in these platy limestones. This is not the place to discuss these phenomena; it is reiterated that these fish remains are absolutely from the same marine beds as the phyllocarids.

In the discussion of the original living space of *Montecaris*, the question of biocoenosis or taphocoenosis demands a paleogeographic review. The investigation of the Devonian reefs in the Rhenish Massif (Jux 1960) indicated, that in the highest lower Devonian (Emsian) a swell was uplifted in the central part of the geosyncline on the flanks of which small reefs settled, extending generally from the Eifel (Text-fig. 1) to the east. These bioherms enlarged to large stromatopore biostromes, when the swell (the Siegerland block) and other smaller ones in its forelands gradually submerged during Givetian times. They all marked the centers of big Hercynian anticlines appearing thereafter. In the Frasnian this epeirogenetic development was accentuated by short periods of regional uplift in the swell centers (=regressions) and subsequent subsidence (=transgressions). These movements have been clearly interpreted by Lecompte in the Ardennes (Text-fig. 1). During Frasnian time first orogenetic phases appear in the eastern parts of the Rhenish Massif.

It is not necessary to state how far the above mentioned swells, which were substantial cause for reef formation, were due to islandlike continental events and where they were located about the borders of the Old Red continent of that period. During the Givetian transgression the Massif of Brabant was submerged. Nevertheless in the vicinity of the Siegerland swell continental influence is readily observed during Middle and Upper Devonian periods with local changes occurring. This is evident by the lithofacies (greywacke, sandstones, sandy shales and red shales) as well as by the biological documentation, which is characterized by the abundant psilophytes; for example, the change of the fauna to a significant littoral character.

The original living place of the fish fauna in the Strunde valley is not considered here. It may be noted that the platy limestones of Bergisch Gladbach have their limit to the south exactly at the edge of the Siegerland mass, overthrusting with its anticlinal systems of Bensberg, deep Couvinian rocks as well as those of the Lower Devonian (Text-fig. 2). There is no direct evidence as to the development and facies of the southernmost platy limestones (Jux 1956, 1960).

A true biocoenosis may be indicated because of the excellent preservation of *Montecaris lehmanni*, for it would not be generally

expected in a very long drift. Observations on the Gulf Coast of America show that *Limulus* may keep all its segments together even though severe storms and turbulent waters affect it on the beach. Therefore, in the less turbulent water of the platy limestones deposition the mode of preservation is not challenged. Postulating an original marine life are the phyllocarid "teeth" indicated by Schmidt from the Dorp limestone, for their more abundant occurrence seems to call for this condition as in reefs of today in which organisms do not grow under direct continental influence.

It is of interest that different animal groups living in similar zones show exceptional similarities with *Montecaris* which are expressed in a broad, horseshoe-shaped convex dorsal shield and a simple abdominal part. This phenomenon is not only significant in arthropods but it is also visible in primitive fish, being especially clear in *Rhyncholepis*, *Trematapsis*, *Cephalaspis*. *Pteraspis* even has a "rostrum" projecting frontally. In the arthropods this is a common feature. It is clearly developed in the Xiphosura and Gigantostraca, chelonellides and trilobites, in Nebaliacea, the copepodes and the branchiopodes.

The similar living space resulted in adaptations that make a systematic position sometimes difficult to determine when considering only incomplete remains.

SYSTEMATIC POSITIONS OF *MONTECARIS*

Montecaris was identified in this report as a genus of the Rhinocaridae. The order (Packard 1879) corresponds to the Archaeostraca Claus 1889, intergrading with the Nebaliacea Calman to the Malacostraca. In other words, the recent Nebaliacea are a related group to the bulk of fossil phyllocarids and together they are combined among the superorder Leptostraca Claus 1880.

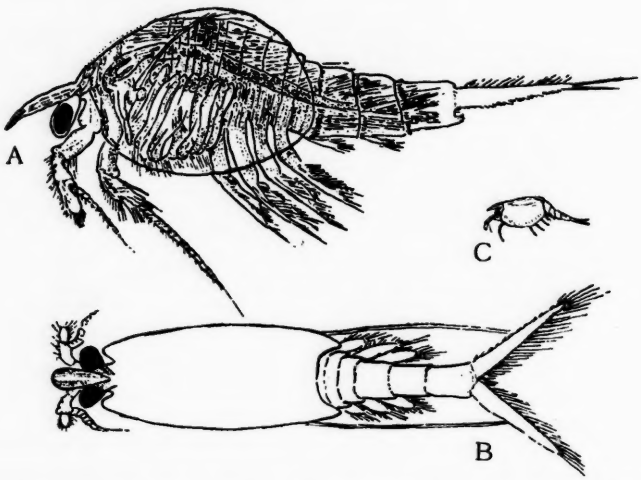
The main features of Leptostraca may be summarized only with regard to living forms: Carapace having a mobile rostral plate, seven pleonites and a telson with furca, stalked eyes, foliated pereiopodes, four pairs of biramous pleopodes, two of them reduced and the last without appendages (Roger 1953).

Observing the fossil documentation, one finds that the relation to the Nebaliacea appears only in the similar, but much larger, carapace and in the resemblance of the abdominal region. Only very rarely so-called rostral plates were identified among Ceratiocaridae. As to the appendages little is known about them today. Claus points out the totally uncertain relation, which means that the fossil remains have little or no relation to the *Nebalia* Leach but that these forms have been types of Crustacea of which no living representative is found. Pompeckj also mentioned the wide gap in documentation between present time and the Carboniferous, which in his opinion excludes a direct relationship.

A fossil directly identifiable with the genus *Nebalia* was found in the Permian of the lower Rhine valley (Malzahn 1958). Its abdominal region and pleopods of the minute specimen corresponded so closely with the diagnosis of the genus that the old organization already emphasized by Leach and Claus find an excellent geologic attestation. The documentation of Nebaliacea remains therefore appears to be proved down to the Paleozoic and by that in the same way assures the nearly unchanged survival of a genus for some 200 million years.

As to the living space of the recent Nebaliacea (*Nebalia bipes*, North Sea and Mediterranean; *Nebaliella*, bathypelagic) there are, because of the enormous dissemination of the cosmopolitan group, naturally analogues which can be reconstructed to the fossil phyllocarids; however, the critical comparison of the Recent form (Text-fig. 7ABC) showed that abdomens ending with a furca and extending behind a posteriorly open valve are generally signs which concern only systematic speculation.

Nearly all the fossil forms appear to have distinct and significant sculptures on the dorsal shield, which usually has a much flatter curvature than *Nebalia*. All the phyllocarids do possess a characteristic central spine in the telson which is flanked by two lateral spines. The number of abdominal somites is very changeable and completely different from *Nebalia*. There is no fossil phyllocarid currently exposing the appendages mentioned—or even closely related



TEXT-FIG. 7—*Nebalia geoffroyi* M. Edw. (after Claus 1872). *A* = female and *B* = male, *C* = natural size.

mandibles or maxillaries. On the contrary, the abdominal somites of the phyllocarids do not possess the significant four pairs of biraminous pleopodes followed by two pairs of more reduced pleopodes; yet all the abdominal rings are without segmented appendages.

The mandibles are, in contrast to *Nebalia*, developed as powerful toothlike structures. Cases where phyllocarids are preserved with their "antennae" are very strange. The differences between Nebaliacea and phyllocarids have been emphasized enough even completely disregarding the contrasting dimensions between them.

Phyllocarids are not easily brought into connection with Nebaliacea, not even with the help of the "rostrum" of some Ceratiocaridae. From the lower Devonian shales of Victoria (Australia) Sherrard (1930) recorded as *Hymenocaris ornata* a badly preserved fossil specimen which may not be identified with certainty as a phyllocarid. Nevertheless, a "rostrum, stalked eyes, cephalic appendages, cercopods and uropods" were interpreted. There are unfortunately more such cases.

It is astonishing that up to the present time the phyllocarids have been systematically grouped in the demonstrated way. The position of the Recent Nebaliacea among the Malacostraca is established without any doubt, and as early as 1909 Gerstaecker & Ortmann pointed to the fact that none of the known fossil remains appears to have any recognizable structure that allows a direct or near association with the Nebaliacea of today.

COMPARISON WITH THE ENTOMOSTRACA

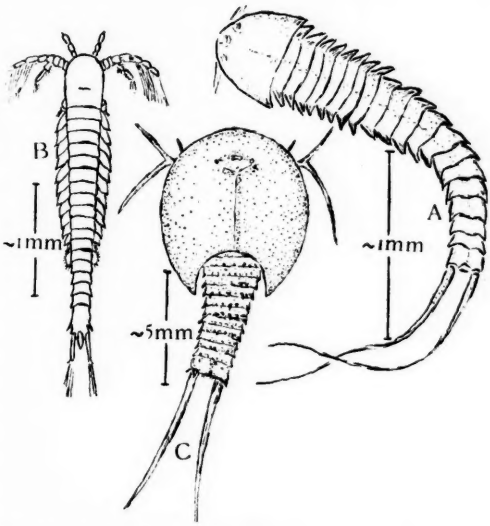
"The oldest Crustacean known today is *Hutchinsoniella*, a resident of American east coast waters. Only 1/10 of an inch long it links modern Crustacea such as shrimps, lobsters, crabs, etc. with their extinct ancestors" (Barnett 1954). Indeed, this very minute crustacean, scientifically investigated by Sanders only in 1954, is a primitive and generalized form. In "Life" Barnett (1959) even mentions: "*Hutchinsoniella* has features in common with both existing Crustacea and the long extinct trilobites." This is a bit more carefully expressed, however, by Sanders (1955), as "*Hutchinsoniella* may be looked upon as an extremely primitive crustacean at about the same level of complexity as the Branchiopoda but probably related to the ancestral stock that gave rise to Copepoda, Branchiura and possibly the Malacostraca."

Hutchinsoniella possesses a horseshoe-shaped shield producing backward, over the first thoracic segment, 2–9 postcephalic segments, which extend posteriorly at the sides as well developed pleura, 10 succeeding abdominal segments bearing pleural spines and a telson with caudal furca armed with very long setose spines. Eyes are absent.

Associated with the branchiopods are the great number of thoracic and abdominal segments, the absence of pleopodes and the abdomen, the occurrence of the furca, the mode of reproduction, the presence of gnathobases on all the thoracic appendages and the development of the mandibles. Because of the appearance of thoracic appendages, which are much nearer to the ideal birameous appendages than the posterior thoracic segments of *Lepidurus* (Text-fig. 8AB), Sanders discards *Hutchinsoniella* from the branchiopods.

The correspondence of *Hutchinsoniella* to *Lepidocaris rhyniensis* Scourfield, an anostracan reaching only a few millimeters and having been detected in middle Devonian limnic deposits of Rhynie, is so significant with regard to the development of the cephalic region, numbers of segments, and their arrangements (Text-fig. 8AB) that a closer relationship of both the specimens seems very evident. Similar to this is the case of the *Gilsonicaris* from the Hunsrück shales, described by van Straelen (1943). A really gigantic specimen that originally extended more than 10 cm. and also indicated some affinities to *Hutchinsoniella* was studied by Brooks (1955). It is of some importance in that this *Tesnusocaris goldichi* Br. has prominent sessile faceted eyes situated on the dorsal shield near its frontal region.

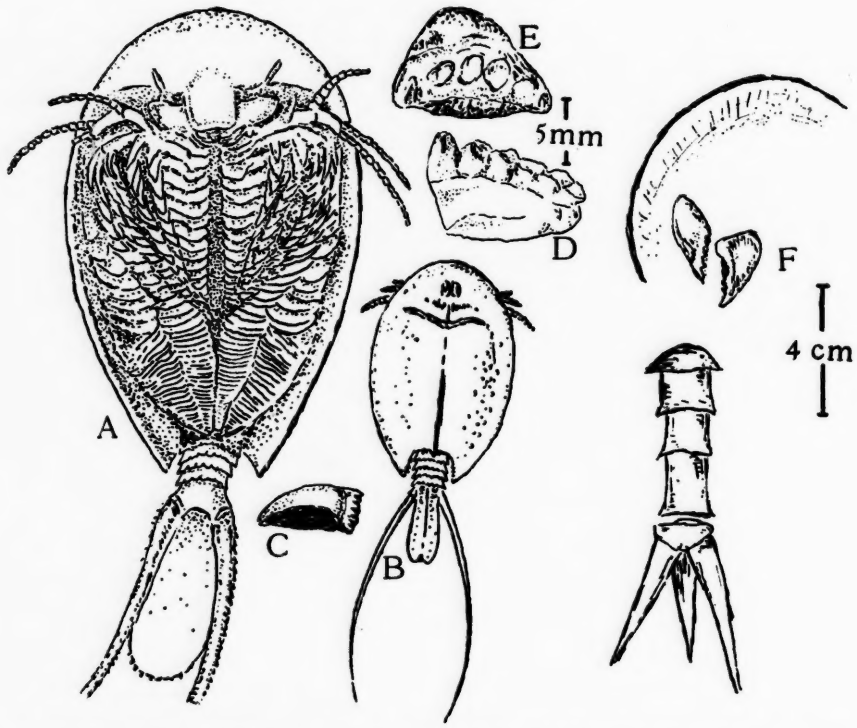
The location of the eyes, however, closely resembles the development on the carapaces of Notostraca. Here some specimens prove to have similarities to fossil phyllocarids as *Lepidurus* or *Apus*, *Apodites* and the often discussed *Protocaris;* yet A. Gerstaecker touched upon this question in 1866–1879 and concluded that on account of the described fragments of *Ceratiocaris* it could be stated with absolute safety that these fossils were not branchiopods. In his opinion a tripartite terminal segment should exclude the relation with recent branchiopods;



TEXT-FIG. 8—*Hutchinsonielle* (*A*), *Lepidocaris* (*B*) and *Apus cancriformis* (*C*), three primitive branchiopods of Triassic (*C*) and Recent times (after Barnett 1959, Scourfield 1945, Trusheim 1938).

however, this criticism will lose its validity if the abdominal development of *Lepidurus productus* (Bosc.) is observed. Here (Text-fig. 9AB) a spade-shaped prolongation of the last abdominal ring is present, which has a significant dorsal keel that is directly comparable, without hypothetical constructions, with the central spine of the phyllocarids, being in the same way flanked by two longer lateral spines. With regard to the dimensions, as argued by Gerstaecker, there is in Apodidae a wide field of relationships to many phyllocarids. Gigantic specimens are to be found in all the animal groups. Concerning the free posterior abdominal rings, Text-figure 9AB clearly portrays the correspondence to the phyllocarids.

Significant information is presented in the carapace. In *Apus* and *Lepidurus* of today these are the frontal two-thirds of the animal which are covered dorsally by a thin chitinous shell. The dorsal surface of this valve often is characterized by a median keel, dividing both halves of the shield in two equal parts. The paired eye-pits are situated very close to this rim and in its foremost frontal region (Text-fig. 9B). Im-



TEXT-FIG. *9—Lepidurus productus* (Bosq.), ventral and dorsal view (*A*, *B*) and the mandible (*C*) of *Apus* compared with the isolated "teeth" of *Dithyocaris* (*E*, *D*) and those still *in situ* of *Echinocaris punctata* Hall & Clarke (*F*) (after Cuvier, Jones & Woodward, Hall & Clarke).

mediately frontal to it there is a median eye and behind a semitransparent oval area, the dorsal organ. Slightly posterior to the dorsal organ occurs a shallow furrow, the cervical fold; behind it appear a pair of coiled tubes, the shell glands.

The cervical fold marks the region where the animal body has its fixation; behind it follows the free attached segmented thorax and finally the abdomen. In the frontal region the dishlike carapace bends down, turning backward, and the "ventral surface of the head is formed by a flattened subfrontal plate, continuous marginally with the carapace. The posterior edge of this plate is convex backwards and is produced in the middle line into a shield-shaped process, the labrum or upper lip (Text-fig. 9A) which overhangs the mouth" (Parker & Haswell 1947, p. 387–388).

Apodidae have been found among fossils too. Schindewolf (1950) emphasized *Apus cancriformis* as probably the "long-lived" species, for this species has been found in great numbers in the Upper Triassic of southwest Germany, and the excellently preserved fossils showed only a very slight differentiation (Trusheim 1938). The number of abdominal segments is variable, this being common in the family.

From the Permian of Oklahoma, Ruedemann (1922) describes *Apus beedei*. Although only undistorted carapaces were found, they clearly show impressions of the shell glands.

To be certain the evolution of branchiopods similar to Apodidae will reach further back into geological time, it is to be remembered that the Cambrian specimens such as *Protocaris marshi* Walc., *Marella splendens* Walc., *Burgessia bella* Walc., *Hymenocaris perfecta* Walc. and *Carnarvonia venosa* Walc. are always brought to the discussion of branchiopods.

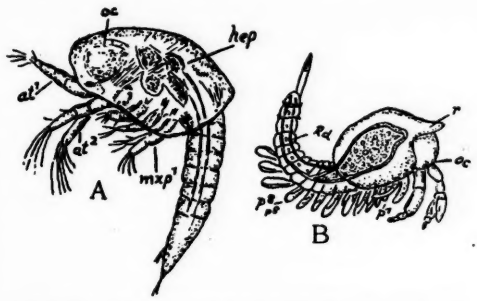
LIVING HABITS OF APODIDAE

Apus and *Lepidurus* are actually living in freshwaters of most parts of the world; however, they do not occur abundantly and their distribution is very changeable. Trusheim (1931) studied the behavior of *Apus cancriformis* (= *Triops cancriformis*) in a pool that was drying out and he gathered very valuable actuo-paleontological data. In stagnant waters the dead animals were laying mainly on their dorsal shields showing that they swam in such a way as to ventilate the water with their appendages. Many Apodidae dug themselves into mud when water was diminishing, thus suffocating in a lifelike position.

Reviewing the fossil assemblage of *Echinocaris socialis* Hall & Clarke (1888, Pl. 30, fig. 9) relations similar to those described by Trusheim should come to mind; however, these specimens were found together with trilobites. The observed Apodidae of Triassic age were found only in a continental facies and they lived exactly in the same habit as their representatives do today. The possibility was discussed that *Montecaris* possibly might have drifted from a primarily continental area into the marine basin; however, the great amount of the other phyllocarids indicates a predominantly marine environment. This question was intensively discussed on Syncarida (*Palaeocaris*) and Branchiopoda by van Straelen and he points to the analogies to be seen in the ganoid fish.

MONTECARIS, A BRANCHIOPOD CRUSTACEAN RELATIVE OF NOTOSTRACA

The organization of Notostraca shows considerable resemblance to *Montecaris*, considering the general anatomy of the body documented in fossils. The resemblance is also manifested in development of the abdomen which does not have a fixed number of somites and is also observable in the telson (= *Lepidurus*). These are characteristic features no longer observed in Nebaliacea. *Nebalia* is a very malacostracan crustacean, and the higher classification with branchiopods results from the fact that *Nebalia*, like all Malacostraca, passes a *Zoaea*-stage



TEXT-FIG. *10*—*A*, "*Calyptopis*" Zoaea of *Nyctiphanes australis* (after Spence-Bate *in* MacBride 1914); hep = liver lobules; oc = compound eye. *B*, *Nebalia* larva (after Gerstaecker 1901); r = rostrum; oc = eye.

when a larva, while Apodidae develop from the *Nauplius* (Text-fig. 10B).

While the carapace of the Nebaliacea is smooth and not especially sculptured, it is modeled in the Apodidae in a way that strictly resembles the fossil phyllocarids. The most significant point is the dorsal furrow in the anterior third of the shield. There in Notostraca the segmented thoracal part comes to an end and follows the cephalic region. From there the animal body is free backward. There is a good number of specimens that prove that this was much the same in fossils. Only the descriptions of Jones & La Touche (Pl. V., fig. 1), *C. salteriana* J. & W. (Pl. VII, fig. 3), *C. laxa* J. & W. (Pl. VII, fig. 12) and *C. papilio* Salt. (Pl. XII, fig. 2a) may be named. The dorsal furrow proves to be a very valuable trait, as it shows important relations to the inner anatomy.

However, the sculpture of the anterior dorsal shield indicates parallels to the Apodidae also. *Echinocaris crosbyensis* Eller (1935) shows next to the median suture in the frontal half of the valve a row of three slightly elevated nodes that are found again, not so sharply profiled, in *Montecaris* (Text-fig. 4AB), *Echinocaris*, *Aristozoe* and others. These nodes were interpreted differently in literature, in part as eye notches, then when nothing similar to it was observable in Nebaliacea as muscle impressions (Richter 1933), as spawn-bulge etc. It followed that in *Nahecaris stuertzi* Jaeckel the "stalked eye" next to the "rostrum" was interpreted

as occurring in a nodular pyrite concretion. Broili's reconstruction (Text-fig. 5C) terminated in such a manner that the specimen completely resembled the Recent *Nebalia*. The final abdominal segment runs out in spines having an inner margin of setaceous fimbriae, the abdominal rings are comparable in number with *Nebalia* (Text-fig. 7), pleopods appear, and the antennae with their biramous construction resemble *Nebalia*.

Intensive comparisons shall not be attempted on the characteristic sculpture of the phyllocarid valve anterior to the shallow furrow with the Apodidae; however, it is very probable that many of the eye notches mentioned in literature (*Mesothyra*, *Tropidocaris*, *Elymocaris*, *Echinocaris* etc.) really were the original sites of the eyes. Thus they are similarly observable in the recent Apodidae or even in *Limulus*. There is much indication that many phyllocarids represent a stage of evolution when the visible organ shifted forward below the dorsal shield finally to reach a position as in *Nebalia*. Such a stage seems most probably to have existed and it is visible even today in the "*Calyptopsis*"-*zoaea* of *Nyctiphanes australis* (Text-fig. 10A) while the larva of *Nebalia* indicates a further step forward (Text-fig. 10B).

Should this really be the case, the recent Apodidae would represent in this respect a more primitive position than the more progressive phyllocarids, and their forerunners might have been a group being somewhat featured in the "*Cypris*"-larva or pupa of *Lepas fascicularis* (MacBride 1954).

The posterior area of the *Echinocaris crosbyensis* carapace (Text-fig. 4B) is swollen and covered with small tubercles. There is little doubt that the position of the shell glands or excretory organs is shown as being very prominent in Recent Apodidae and often marked among the fossil material by lateral bulges or keels.

This summary proves that considering abdominal development and sculpturing of the dorsal shield, there are many marked relationships between phyllocarids and Notostraca and it shows clearly that they are far from being joined to the Nebaliacea.

What may be stated as to the ventral anatomy of the phyllocarid body? It already has been emphasized that the convex dish-like valve in natural form originally bent down and backward, so that frontally a minute peak confusable with a rostral plate was developed. Text-figure 3B gives the probable reconstruction of the valve of *Montecaris*. The "rostrum" was taken into consideration and it is taken to be somewhat hypothetical in the genus. The excellent preservation of this plate in *Ceratiocaris papilio*, however, clearly shows the correspondence with the Apodidae and again emphasizes the differences in *Nebalia*. This subfrontal plate covers vigorous mandibles in *Apus* and *Lepidurus* and there are good reasons to believe that it was entirely the same in phyllocarids. To prove this a convincing fossil documentation may be drawn.

Looking first at the specimens described as phyllocarid "teeth" in the classic records of Jones & Woodward (1888–1889) or even Hall & Clarke (1888), one might say that all discussion pointing out the correspondence to the Recent shape of *Apus* and *Lepidurus* mandibles is superfluous. Attention may be paid only to their comparison on Text-figure 9CED. Phyllocarid mandibles are not to be taken as *problematica*, as is proved by some findings of *Dithyrocaris* (Hall & Clarke 1888, Pl. XXVIII, figs. 4–5). These specimens still have their mandibles in the natural position, but on the other hand nothing is preserved of the appendages (Text-fig. 9F). It is really very astonishing that Hennig, describing *Nahecaris stuertzi* Jaeckel, did not observe these relationships to the Notostraca; for he worked on two specimens showing on the marvellously prepared ventral side the mandibles (he identified them with the maxillae) in their original place, so that others might not be difficult to determine. The correspondence with *Apus* and *Lepidurus* is significant in these remains (Hennig 1921, Pl. 33, fig. 1a; Pl. 34, fig. 1a) because abdominal feet, mandibles and gnathobases are clearly identifiable. It is confusing that Richter and Broili referred this species to the Leptostraca, totally ignoring the anatomic situation and following only the tradition of palaeontologists.

The reconstruction of the anterior ventral part of *Montecaris* (Text-fig. 3C) is strik-

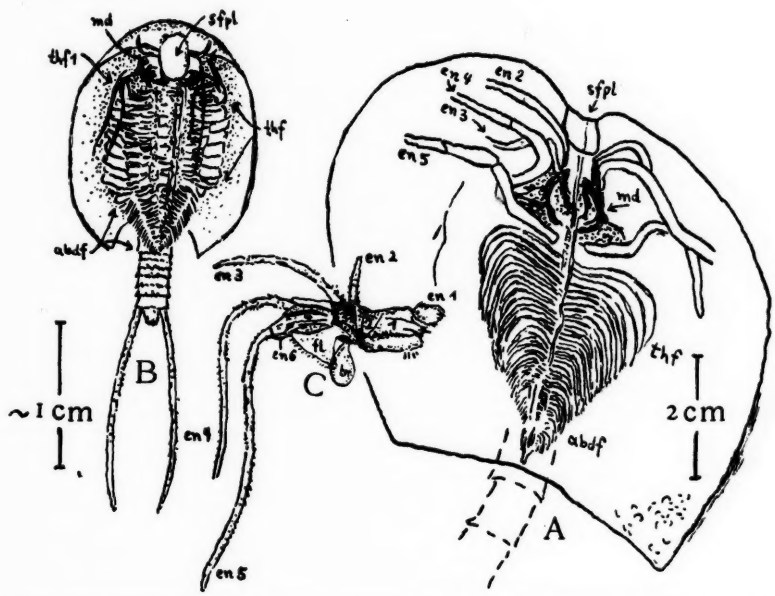
ingly similar to *Lepidurus*. The final proof for the conjecture that *Montecaris* and the allied phyllocarids are supposed to be branchiopods similar to *Lepidurus* and *Apus* seems to be in the discovery of *Vachonisia rogeri* Lehmann. These specimens, as well as *Nahecaris* remains, were also found in the lower Devonian Hunsrück shales (Text-fig. 1). Lehmann immediately recognized the similarity to the branchiopods, but he did not discuss the relationships with phyllocarids, as the specimens were originally taken for ones lacking the free segmented abdomen. Now, however, there are so many examples that phyllocarids were preserved only as dorsal shields (so also many nahecarids in the Hunsrück shales), and the carapace of *Vachonisia* is so typically phyllocarid, that there is no doubt about it. The free abdomen was separated from its valve before fossilization.

Comparing the anatomical features of *Vachanisia* and *Apus*, Lehmann discovered by use of a carefully done preparation and X-ray (Text-fig. 11ABC) that, apart from the general shape of the carapace, the subfrontal plate is easily identifiable, as are the development of the 1st thoracic feet and the very clear mandibles, and finally the thoracic feet and the abdominal feet.

A better argument than *Vachonisia rogeri* Lehmann will be hard to find. The systematic examination of the new findings thus means that the branchiopods join Apodidae and Phyllocarida (=Archaeostraca) and that the Leptostraca include only one fossil specimen, *Nebalia bentzi* Malz.

In conclusion, *Montecaris* may be posed systematically in the following manner:

Super subphylum EUARTHROPODA
Subphylum ANTENNATES (MANDIBULATES)
Class CRUSTACEA
Sub-class I BRANCHIOPODA
Order ANOSTRACA, NOTOSTRACA, PHYLLOCARIDA (=ARCHAEOSTRACA), CONCHOSTRACA, CLADOCERA



TEXT-FIG. *11*—*Vachonisia rogeri* Lehmann compared with *Lepidurus glacialis*. *A*, *V. rogeri*: sfpl =subfrontal plate; abdf=abdominal feet; en 2–5=endites of 1st thoracic foot; md=mandible; thf=thoracic feet. *B*, *L. glacialis:* thf 1=1st thoracic foot. *C*, 1st thoracic foot of *L. glacialis:* 1–4=podomeres; en 1–6=endites; br and fl=exites. (Supplemented after Lehmann 1955 and Parker & Haswell 1947).

Family APODIDAE, RHINOCARIDAE Clarke 1903 (not CERATIOCARINAE Clarke 1913) Genus MONTECARIS

A direct union of Archaeostraca and Notostraca may be discussed; however, the phyllocarids remain a various and well defined group, considering only the significant telson, which differs clearly from *Lepidurus* because of the dagger-shaped or spiny development. The position completed in the manner shown seems to be more reasonable. Finally, the living space is most probably different. Phyllocarids are documented as fossils from Lower Cambrian up to Triassic time. During this space of time the remains are always together with marine specimens. Since the Permian, or more specifically since the Triassic, real Apodidae were observed, populating the freshwater pools and ponds of the continents.

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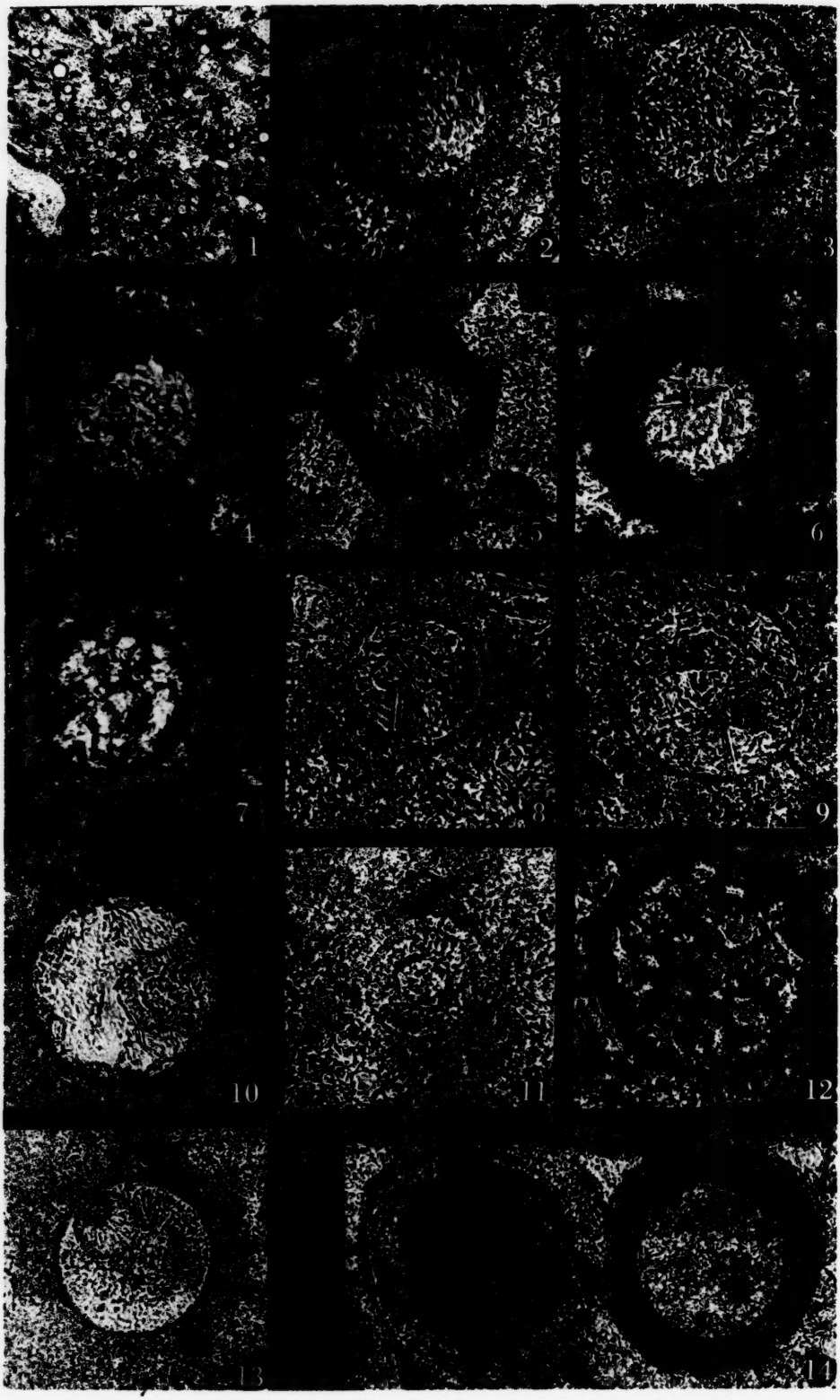
(*Explanation of* PLATE 143 *on next page*)

EXPLANATION OF PLATE 143

FIG. *1*—*Montecaris lehmanni* Jux, n. sp. Cotypus and counterpart of the holotypus figures on Pl. 142, fig. 1. Collection: Geol. Surv. Northrhine Westfalia, Inv. Nr. GiO 9b.

2—Right valve half of *Montecaris strunensis* Jux. The specimen was torn off from the left half along the median rim. Three notches appear clearly in front of the dorsal furrow and the posterolateral spine. Locality and geologic horizon as in figure 1; detailed dimensions are given in the text. Collection: Geol. Department, Louisiana State University, Baton Rouge.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JOURNAL OF PALEONTOLOGY, V. 34, NO. 6, P. 1153–1157, PL. 144, NOVEMBER, 1960

CALCISPHAERA FROM THE SALEM (MISSISSIPPIAN) LIMESTONE IN SOUTHWESTERN ILLINOIS

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ABSTRACT—Thin sections of the Salem Limestone from outcrops in the Mississippi River bluffs in southwestern Illinois contain tiny, calcareous spheres which are prominent elements in certain types of limestone. These microorganisms are referable to the genus *Calcisphaera* established by Williamson (1880). They vary in size, having diameters of 30 to 165 microns. They occur most abundantly in calcisiltites and calcarenites in which microcrystalline, nonskeletal grains are important rock forming elements. They also occur in calcilutite.

INTRODUCTION

A recent study of thin sections from the Salem Limestone in southwestern Illinois has revealed the presence of minute spherical objects in the formation. The spheres generally consist of clear calcite surrounded by a calcitic wall of variable structure and complexity and are interpreted as fossil remains referable to the genus *Calcisphaera* Williamson 1880.

The Salem Limestone (Spergen of many authors) crops out extensively in the Mississippi River bluffs of southwestern Illinois. It is placed in the Valmeyer Series by the Illinois State Geological Survey, and in the lower part of the Meramecian Series by many others. Typically, the Salem is a medium to coarse biocalcarenite but it also includes beds of microcrystalline limestone and fine-grained calcarenites in which nonskeletal microcrystalline grains are important rock building elements (Baxter, 1960). Locally these beds contain calcified lycopsid plant material and thin coalified veinlets of organic material.

The representatives of *Calcisphaera* de-

EXPLANATION OF PLATE 144

Calcisphaera from the Salem Limestone of Illinois.

FIG. *1*—Fine-grained calcarenite with abundant *Calcisphaera*. Approximately ×30.
2—*Calcisphaera* with thick homogeneous wall structure. Approximately ×300.
3—*Calcisphaera* with double thin walls enclosing numerous cubical compartments. Approximately ×300.
4—*Calcisphaera* with double thin walls. The outer wall is poorly preserved. Approximately ×300.
5—*Calcisphaera* with hexagonal peripheral outline. Approximately ×225.
6—*Calcisphaera* with sphere wall consisting of two parts, an inner double wall with connecting partitions and a thick outer investing layer. The outer layer has a rounded hexagonal outline. Approximately ×225.
7—*Calcisphaera* with thin inner wall and a relatively thick outer layer which is translucent and transected by radial spinelike projections from the inner wall. The outer layer vaguely shows a hexagonal peripheral outline. Approximately ×300.
8—*Calcisphaera* with poorly preserved circular outer layer and spinelike projections from the thin inner wall. Approximately ×300.
9—*Calcisphaera* with thin inner wall and spinelike projections. Approximately ×300.
10—*Calcisphaera* with thin wall and few short radial projections. Approximately ×225.
11—*Calcisphaera* with annular sphere wall construction. Approximately ×300.
12—*Calcisphaera* with sporelike objects within the central cavity. Approximately ×300.
13—*Calcisphaera* with wall structure thought to represent an orifice. Approximately ×225.
14—Two thick-walled *Calcisphaera*. Specimen on right has concentric wall structure and faint radial lines transecting the wall. Specimen on left has central cavity filled with microcrystalline calcite. Approximately ×300.

scribed here were found in an outcrop located a mile southeast of the village of Chalfin Bridge in the SE SW sec. 7, T. 4 S., R. 10 W., Monroe County, Illinois. The limestone exposed along the bluff was sampled at one foot intervals. Abundant *Calcisphaera* were found in thin-sections from fine-grained nonskeletal calcarenites and calcisiltites, (Pl. 144, fig. 1). The thin sections are in the repository of the Illinois State Geological Survey, Urbana, Illinois. Publication is authorized by the Chief, Illinois State Geological Survey.

Genus CALCISPHAERA Williamson, 1880
Type species: *Calcisphaera laevis* Williamson, 1880

The genus *Calcisphaera* was established by Williamson (1880) for a group of microorganisms of uncertain affinities. The generic name was recommended as "not involving any premature hypothesis respecting their nature" (Williamson 1880, p. 521). Williamson recognized six species from the Lower Carboniferous of Wales and a single species from the Upper Devonian of Ohio but did not establish a type species.

Miller (1889, p. 155) designated *Calcisphaera robusta* Williamson, from the Devonian of Ohio, as the lectotype of the genus. *C. robusta*, however, is much larger than the Welsh specimens and is now considered to represent an ancient charaphyte (*Trochiliscus*). Andrews (1955, p. 123) designated *Calcisphaera laevis* Williamson as the type species and this designation is now generally accepted.

Cayeux (1929) considered Williamson's *Calcisphaera* to be divisible into two general types which he called *calcisphères typiques* and *radiolaires calcifies*. The latter evidently refers to *C. spinosa* Williamson in which the sphere wall is thin and "the surface is drawn out into a series of tubercules and spines of very variable number, length, and acuteness" (Williamson 1880, p. 522).

After the establishment of the genus, related calcareous spheres were reported from the Upper Devonian and Lower Carboniferous of France, Belgium, and Germany. Recently, "calcispheres" have been recorded from the Devonian Palliser Formation of Alberta (Beales 1956, p. 857) the Ordovician Black River Group of Ontario, and the Mississippian Rundle Group of Alberta (Beales 1958, p. 1857). *Calcisphères typiques* were reported in the Upper Viséan Kotakigawa Formation of Japan by Konishi (*in* Johnson & Konishi 1956, p. 115) who later found *Calcisphaera fimbriata* Williamson, *emend.* Konishi (*in* Johnson & Konishi 1958, p. 107) in the Devonian Leduc and Cooking Lake Formations of Alberta.

The Leduc and Cooking Lake Formations also contain an organism completely different from *Calcisphaera* Williamson. It has been described by Lombard & Monteyne (1952, p. 14–16) under the name *calcisphère de forme A*. It is characteristically of large size with a thick "prismatic wall" and a bullet-shaped peripheral outline.

CALCISPHAERA FROM THE SALEM OF ILLINOIS

Dimensions.—The diameter of the spheres and the thickness of the sphere walls vary. The former ranges from 30 to 165 microns and the latter from three to 25 microns. This variance is partially due to natural variation in the dimensions of the organisms but to a large extent it is a function of the position of the 30-micron slice of the thin section with respect to the equatorial plane of the individual spheres.

Central Cavity.—The central portion of the sphere is generally occupied by clear calcite. The clear calcite is either in the form of a single crystal which reaches extinction as a unit as the stage of the microscope is rotated under crossed nicols or a mosaic of calcite crystals which reach extinction separately. Some specimens (Pl. 144, fig. 13) have the central cavity filled by translucent, fiberous calcite that is oriented normal to the sphere wall so as to show a crude cross under crossed nicols. A rare form has the central cavity filled with microcrystalline calcite (Pl. 144, fig. 14, left).

Sphere Wall.—The most distinctive feature of the organisms is found in the construction of the sphere wall. Most of the specimens from the Salem have relatively thick walls. Some, however, have walls of only two to three microns thickness. A rare form has a sphere wall that consists of two thin microcrystalline wall layers which are interconnected by a number of transecting radial partitions. Another rare form dis-

plays a hexagonal peripheral outline. A fairly common form is one formed by alternating layers of microcrystalline calcite and translucent, radially oriented calcite.

Orifices.—Most *Calcisphaera* from the Salem appear to lack any type of orifice in thin-section. Plate 144, figure 13, however, illustrates a thin-shelled form which apparently has an orifice.

THICK-WALLED FORMS

Description.—Plate 144, figure 2 shows the structure of most *Calcisphaera* from the Salem. The thickness of the sphere wall ranges from six to 20 microns. The wall is constructed of dark, homogeneous, microcrystalline calcite. Generally, both the outer and inner surfaces of the wall are relatively smooth. In most cases the wall does not have discernible structure but with very high magnification and a darkened field some specimens show radial lines transecting the thick wall. Plate 144, figure 14, right, shows a thick-walled form in which the wall has concentric structure. This and other variations from the more normal form are rare.

Comparisons.—Most thick-walled forms appear to be identical with *Calcisphaera laevis* Williamson (1880, p. 521, pl. 20, fig. 70) but some otherwise identical forms appear to have thin radiating partitions transecting the wall. Derville (1941) combines these forms under the name *Calcisphaera canaliculata* Derville (1941, p. 364, pl. vii, fig. 1–3) with the opinion that the preservation of the *fins canaux* is a fortuitous circumstance.

DOUBLE-WALLED FORMS

Description.—Some specimens have walls constructed of two microcrystalline calcite layers each approximately two to three microns thick and interconnected by radial partitions also formed of microcrystalline calcite (Pl. 144, fig. 3). The partitions are about one to two microns thick and generally four to six microns in length. In cross-section they enclose numerous (20–24) chambers which have been infiltrated by clear calcite. The outer wall layer is rarely complete so that commonly only the inner wall with short, equidimensional projecting partitions is seen, as along the upper periphery of Plate 144, figure 4.

Comparisons.—The forms having double thin walls that enclose partitioned chambers resemble *Calcisphaera cancellata* Williamson (1880, p. 521, pl. 20, fig. 79). It also seems possible that there is a connection between these forms and that portion of the thick-walled forms which fall in the lower part of the six- to 20-micron range of wall thickness.

HEXAGONAL FORMS

Description.—Plate 144, figure 5 is a rare form with a thick wall which is devoid of internal structure but displays a hexagonal peripheral outline. The sphere wall in figure 6 consists of two parts, an inner double wall with connecting partitions and an outer investing layer of microcrystalline calcite. The outer layer has a very imperfect hexagonal outline.

Williamson (1880, p. 521–522) describes two species which show linkage to hexagonal forms. The Salem material includes similarly related types. One such has an inner, homogeneous, dark colored wall layer about three microns thick and an outer, slightly translucent, thick wall layer, which is transected by radial spinelike projections from the inner wall (Pl. 144, fig. 7). The length of the projections and the slight contrast of the translucent layer to the matrix suggest a hexagonal peripheral outline. Figure 8 is similarly constructed but less well preserved.

Another related form has a relatively thin sphere wall with numerous spinelike projections, which have a maximum length of 20 microns (Pl. 144, fig. 9). A few specimens have a simple thin wall without radial projection (Pl. 144, fig. 10) or but a few short ones.

Konishi (*in* Johnson & Konishi 1958) relates such specimens to the hexagonal forms, observing that the hexagonal peripheral outline is achieved only when calcification is complete and a specimen is well preserved.

Comparisons.—*Calcisphaera* having a hexagonal outline appear to be identical with *Calcisphaera hexagonata* Williamson (1880, p. 522, pl. 20, fig. 69), although when the peripheral outline is most apparent the radiating structure described by Williamson is not discernible.

The related types resemble *Calcisphaera*

fimbriata Williamson (1880, p. 521, pl. 20, fig. 67) and possibly *Calcisphaera sol* Williamson (1880, p. 522, pl. 20, fig. 68). *C. fimbriata* Williamson emend. Konishi (1958, p. 107) combines *hexagonata*, *fimbriata* and *sol* into a single species. Konishi states that for the Devonian forms he studied "any specimen examined can be located within a serial change between the two end members of *hexagonata* with hexagonal form and *fimbriata* with circular or elliptic form. Furthermore, more linkage is suggested between *C. fimbriata* and *C. sol* or even to *C. spinosa*." (p. 108).

FORMS WITH ANNULAR WALLS

Description.—A fairly common Salem form has alternating layers of thin, dark colored, microcrystalline, calcite and translucent radially oriented calcite (Pl. 144, fig. 11). The thin walls are about two microns thick and the radial calcite layers about five or six microns thick. A maximum of three or possibly four dark colored layers with two or three enclosed translucent layers occur but in most specimens only remnants of the innermost and outermost microcrystalline layers are preserved.

Comparisons.—Calcispheres of this type are not represented in Williamson's original descriptions. They are similar to *Calcisphaera polyderma* Derville (1941, p. 364, pl. vii, fig. 5) but the microcrystalline layers are thinner than in Derville's specimen and some Salem specimens appear to have an orifice.

ORIGIN OF *CALCISPHAERA*

Calcisphaera have been attributed to a number of diverse organisms. Williamson (1880, p. 525) states that their spherical form suggests the possibility that they may have been the tests of some extinct form of protozoa or "reproductive capsules of some marine form of vegetation." Cayeux (1929) relates part of Williamson's *Calcisphaera* to algal siphons and part to Radiolaria. Konishi (*in* Johnson & Konishi 1958, p. 102) shows that some forms described as *Calcisphaera* are attributable to *Charaphyta* and concludes that "the group of microorganisms which have been referred to *Calcisphaera* is definitely heterogeneous possibly even with the rank of family or higher taxon" (p. 103). Chapman (1921, p. 336) felt that the evidence favored a relationship to calcareous algae such as rhabdospheres and coccospheres. Reynolds (1921) and Kaisin (1910) attribute them to foraminifera and Derville agrees for *C. canaliculata* Derville (1941, p. 364). Lombard & Monteyne (1952, p. 21) think that the most reasonable hypothesis is that they are related to algae of which they are spores.

Pia (1937, p. 803) suggests that in the majority of cases one deals with an inorganic structure formed about a bubble of air trapped in the calcareous sediment and ultimately filled with calcite.

The present study does not give conclusive evidence on origin although a single spherelike object was seen which in cross-section appears to contain smaller spheres within the central cavity. This specimen, shown in Plate 144, figure 12, has a diameter of 86 microns and a relatively thin sphere wall. The smaller spheres are roughly circular and have a diameter of 18 to 20 microns. Possibly this specimen preserves some sort of reproductive capsule.

SUMMARY AND CONCLUSIONS

Salem *Calcisphaera* occur most abundantly in fine-grained calcarenite in which nonskeletal, microcrystalline grains are important rock-forming elements. They also occur in calcilutite. The morphology of Salem forms is similar to some of Williamson's original species. They vary in size and differ mainly in the structure of the sphere wall. Some forms which differ in appearance owe their differences to fortuitous circumstances of calcification and preservation.

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EARLY LUDLOW GRAPTOLITES FROM THE ASHLAND AREA, MAINE

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ABSTRACT—An assemblage of graptolites characteristic of the Early Ludlow zone of *Monograptus nilssoni* is recorded from the vicinity of Ashland, Aroostook County, Maine. The zone of *M. nilssoni* may be correlated with the latter part of the Niagaran. Most of the forms in the assemblage are monograptides of the *dubius-vulgaris-tumescens* groups. One new species, *M. forbesi*, and two new varieties, *M. tumescens* var. *contus* and *M. vulgaris* var. *ashlandensis* are described.

INTRODUCTION

A FEW Silurian graptolites have been recorded from several scattered localities in northern Maine (Ruedemann, 1947), but no extensive fauna has been described from any one locality. It is the purpose of this paper to describe and discuss one fauna from the vicinity of Ashland, Maine.

Many of the earlier collections were the result of the enthusiastic efforts of the amateur naturalist Olaf Nylander. Following in his footsteps is W. H. Forbes, to whom the writer is indebted for sending him the specimens described herein. The writer also wishes to thank Owen Poe for the illustrations.

The collection was made in a roadcut on State Highway 227 (Text-fig. 1) 10 miles in a straight line northeast of Ashland, Maine. Only the graptolites have been studied; however, Forbes states that a nearly complete crinoid was also obtained from the same locality. The fossils occur in a tan, thinly laminated, cross-laminated, very fine grained sandstone that has some thin calcareous interbeds. The fossil-bearing rocks have not been assigned a formation name. Twenhofel (1941) reviewed the Silurian stratigraphy of the region near Ashland, but the fossil locality is approximately 3 miles north of the area encompassed by his study.

AGE

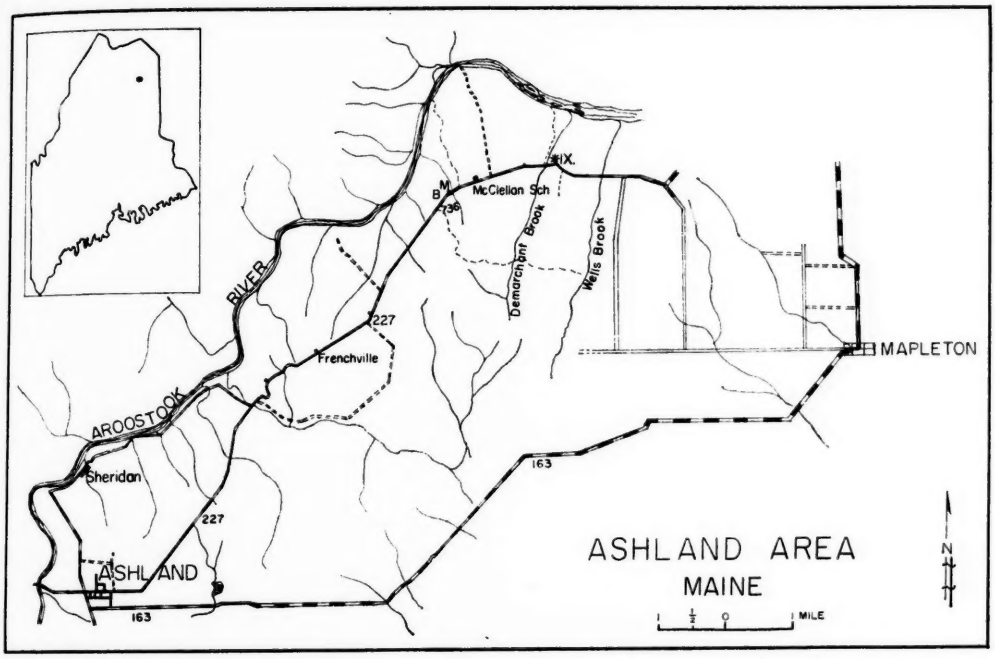
The following list of forms was recognized in the collection:

Desmograptus cf. *D. micronematodes* var. *quebecensis* Ruedemann
Plectograptus sp.
Monograptus colonus (Barrande)
M. dubius (Suess)
M. forbesi Berry, n. sp.
M. tumescens var. *contus* Berry, n. var.
M. vulgaris var. *ashlandensis* Berry, n. var.
M. sp.

The most common species in this collection is *M. dubius*. Large numbers of long, robust rhabdosomes of this form crowd most of the bedding surfaces.

Of the listed forms, only two, *M. colonus* and *M. dubius*, have widespread geographic distribution. *M. colonus* is restricted to the Early Ludlow zone of *M. nilssoni* in the British Isles, Czechoslovakia, and Germany. *M. dubius* is a long-ranging species, having been recorded from the Wenlock zone of *M. riccartonensis* to the Early Ludlow zone of *M. scanicus* in the British Isles. However, Elles & Wood (1910) state that the largest forms of this species occur in the Lower Ludlow shales. Pribyl (1944) indicates that the typical form of this species occurs only in the zone of *M. riccartonensis* in Czechoslovakia. Munch (1952) shows the species to have a similar occurrence in Germany as in Czechoslovakia.

The genus *Plectograptus* is shown to range from the Middle Wenlock zone of *Cyrtograptus rigidus-C. perneri* through the zone of *M. nilssoni* by Boucek & Munch (1952). The new species *M. forbesi* is closely related to the *M. dubius* group which is predominantly Middle Wenlock to Lower Ludlow in age range. All known forms of *M. vulgaris* are restricted to the zone of *M. nilssoni* except the typical form of *M. vulgaris*, which has a range in the British Isles from the latest Wenlock zone of *Cyrtograptus lundgreni* into the earliest Ludlow zone of *M. vulgaris*. All forms of *M. tumescens* are restricted to the zone of that name in Czecho-



TEXT-FIG. 1—Index map of the Ashland area, Maine, showing the fossil locality (IX).

slovakia and Germany, but they range from the zone of *M. nilssoni* through the zone of *M. tumescens* in Britain.

From this discussion of ranges, the writer concludes that the assemblage of forms from the Ashland area is most like a British assemblage from the zone of *M. nilssoni*. The fossils are considered to be representative of that zone and to indicate an Early Ludlow age for the rocks bearing them.

CORRELATION

The writer (1958) discussed the widespread occurrence of the *M. nilssoni* zone in North America. Its most significant appearance is in the Henryhouse shale in Oklahoma where it is associated with a shelly fauna. Amsden (1958) concluded that the Henryhouse and Brownsport formations were correlative. Lowenstam (1940) demonstrated the presence of the Brownsport formation fauna in the basal beds of the Racine dolomite or in the highest of the Waukesha dolomite. The Racine dolomite is considered the correlative of the Lockport dolomite in New York.

Thus the occurrence of the *M. nilssoni* zonal assemblage in the Henryhouse shale permits correlation of this graptolite zone with the North American standard Silurian section. Further, it gives an accurate tie to the type Silurian and indicates that the upper part of the Niagaran series is Early Ludlow in age.

SYSTEMATIC DESCRIPTIONS

Class GRAPTOLITHINA Bronn
Order DENDROIDEA Nicholson
Family DENDROGRAPTIDAE Roemer *in* French
Genus DESMOGRAPTUS Hopkinson, 1875

DESMOGRAPTUS cf. D. MICRONEMATODES QUEBECENSIS Ruedemann

In the description of *Desmograptus micronematodes* (Spencer), Ruedemann (1947, p. 223–224) described and figured (pl. 23, figs. 4–6) a new variety of that species on material collected from a Silurian sandstone at Black Cape, Quebec. He named the new form *D. micronematodes* variety *quebecensis*. Ruedemann's description of the variety is as follows: "It shows a flabellate rhabdosome, 7 cm. wide in the middle and 4 cm. high.

Branches slightly undulating and connected by dissepiments (some broad and bandlike) in proximal portion and more strongly undulating and anastomosing in distal portion. Branches very delicate, only 0.25 mm. broad; meshes quadrilateral in proximal portion and rhomboidal in distal portion, they vary from 1–3 mm. in length, 10–14 in 10 mm. transversely." He also stated that the thecae appear as slender tubes 7 to 8 times as long as they are wide, and that they number 16 in 10 mm.

The specimens from the Ashland area are fragmentary and no complete rhabdosomes were found. The fragments do have undulating and anastomozing branches that are 0.25 mm. wide. The meshes are rhomb-shaped, are 2–3 mm. long, and number 7 in 5 mm. Thecae were not seen.

Order GRAPTOLOIDEA Lapworth
Family RETIOLITIDAE Lapworth
Subfamily PLECTOGRAPTINAE
Boucek & Munch
Genus PLECTOGRAPTUS Moberg & Tornquist, 1909
PLECTOGRAPTUS sp.

A few broken fragments of rhabdosomes which may be referred to the genus *Plectograptus* are present in the collection. One of these forms is 13 mm. long and 4 mm. wide. No reticula are present in it. Diagonal lists form a vertical zig-zag line approximately in the middle of one side, and horizontal connecting lists go out from the corners of the diagonal lists to the pleural lists that delimit the lateral walls. Hexagonal areas are delimited where the horizontal and pleural lists join. These areas number 11 in 10 mm.

This form resembles *P. macilentus* (Tornquist) in general pattern of the lists. However, it is wider and has more hexagonal areas in 10 mm. than *P. macilentus*, and the proximal end is not present. Specific identification is not possible because the rhabdosome is incomplete.

Family MONOGRAPTIDAE Lapworth
Subfamily MONOGRAPTINAE Lapworth
Genus MONOGRAPTUS Geinitz, 1852

The writer follows Bulman (1955) in including as synonyms here the several generic names (*Pristiograptus*, *Monoclimacis*, etc.) proposed for groups considered subgeneric in taxonomic rank. For a discussion of the reason behind this opinion, see Bulman, 1955, p. V69.

MONOGRAPTUS COLONUS (Barrande)
Text-fig. 2F

Graptolithus colonus BARRANDE, 1850, Graptolites de Boheme, p. 42, pl. ii, figs. 2,3.
Monograptus colonus Barrande. TULLBERG, 1883, Skanes Graptoliter, pl. i, figs. 22,23, ELLES & WOOD, 1910, Palaeontographical Soc., Mon. Brit. Graptolites, p. 391–393, text-figs. 260a-c, pl. XXXVIII, figs. 8a-d.

Description.—The rhabdosome is 4 to 6 cm. in length and widens gradually from 0.5 mm. initially to a maximum of 2.2 mm. It is straight distally but has a distinct ventral curvature proximally.

The thecae number 11 to 12 in 10 mm. The first four thecae have an ogee curvature of the ventral wall and retroverted apertural extremities. The other thecae are simpler and the distal ones are straight tubes that are approximately four times as long as they are wide, overlap nearly two-thirds their length, and are inclined at a 30 to 40 degree angle.

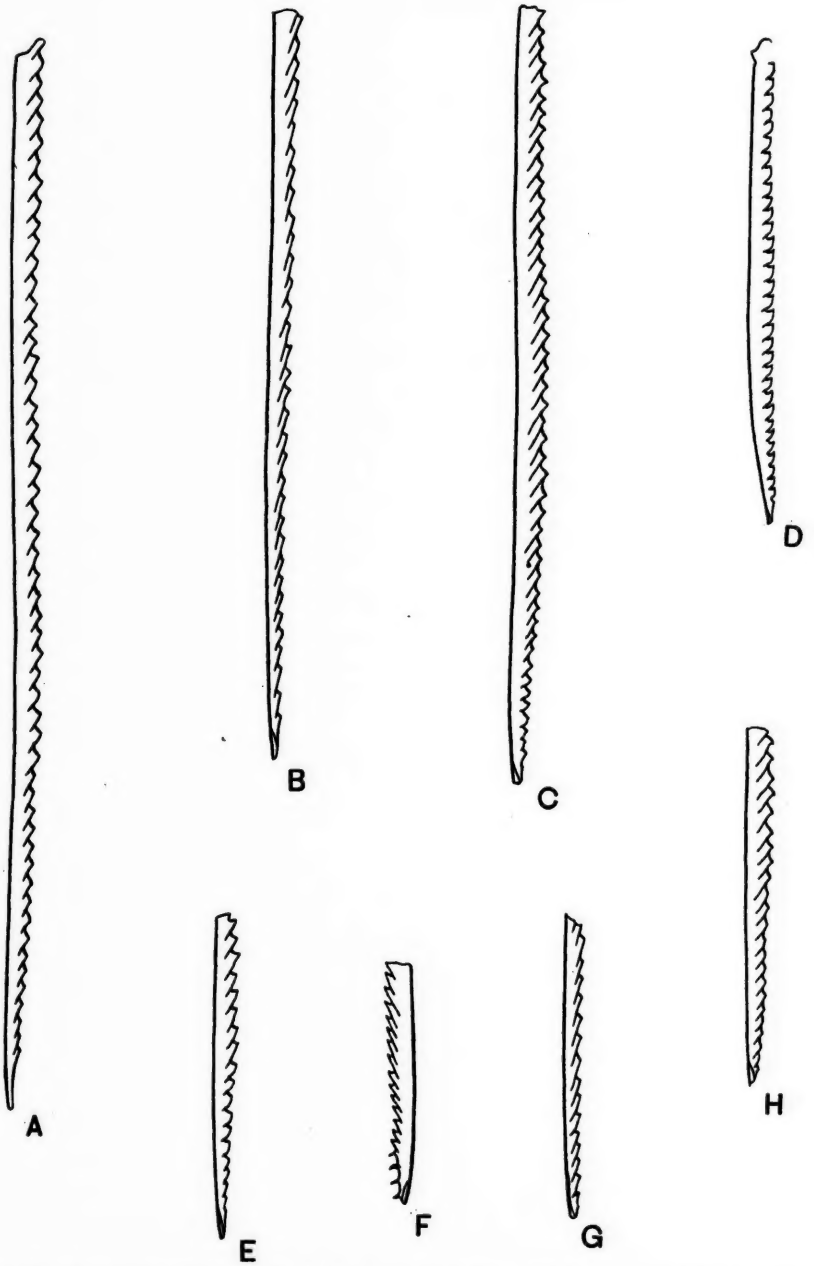
The sicula is small and slender. Its apex attains the level of the second thecal aperture.

MONOGRAPTUS DUBIUS (Suess)
Text-figs. 2A,2E

Graptolithus dubius SUESS, 1851, Ueber bohmische Graptolithen, Haidinger's Abhandl. v. iv, pt. iv. p. 115, pl. ix, figs. 5 a,b.
Monograptus dubius LAPWORTH, 1876, Geol. Mag., dec. ii, v. iii, p. 506, pl. xx, fig. 10, ELLES & WOOD, 1910, Palaeontographical Soc., Mon. Brit. Graptolites, p. 376–378, text-figs. 247a,b, pl. XXXVII, figs. 7a-d.
Pristiograptus dubius dubius PRIBYL, 1944, Akad. Tcheque des Sciences, Bull. Internat., v. 44, p. 36–37, Taf. I, Abb. 4–6.

Description.—The rhabdosome is 8 to 9 cm. long, is straight distally, but has a slight ventral curvature in the proximal region, and widens gradually from an initial width of 0.7 mm. to a maximum of 2 mm.

The thecae are straight tubes which are two to three times as long as they are wide. They overlap for approximately one-half their length, and they are inclined to the stipe at an angle of 30 to 35 degrees. They number 8 to 11 in 10 mm. The apertural margins are commonly thickened to form a



TEXT-FIG. 2—Outline drawings of Early Ludlow graptolites. All figures are ×2. *A*, *Monograptus dubius* (Suess), nearly complete rhabdosome, UCMP 37722; *B*, *M. forbesi* Berry, n. sp., holotype, UCMP 37718; *C*, *M. tumescens* var. *contus* Berry, n. var., holotype, UCMP 37720; *D*, *M.* sp., UCMP 37725; *E*, *M. dubius* (Suess), proximal portion of rhabdosome, UCMP 37723; *F*, *M. colonus* (Barrande), proximal portion, UCMP 37724; *G*, *M. forbesi* Berry, n. sp., proximal portion of paratype, UCMP 37719; *H*, *M. vulgaris* var. *ashlandensis* Berry, n. var., holotype, UCMP 37721.

distinct flange which, upon compression, yields a blunt denticle.

Remarks.—Most specimens from the Ashland area agree fully with the description. Some exhibit a slight dorsal curvature in the median or distal portion of the stipe but this appears to be the result of bending along an irregular surface during burial. In addition, some specimens are present in which the maximum length is 10 cm. but they agree in all other aspects with the description. In yet other specimens, the maximum breadth is 2.2 mm. but they, too, agree in all other aspects with the description of the typical *M. dubius*. These latter two forms might be referred to Pribyl's variety (1944, p. 37–38), *P. dubius latus*, except that the thecae number 8 in 10 mm. distally and 10 in 10 mm. proximally, whereas Pribyl states that the thecae always number 8 in 10 mm. in *P. dubius latus*. Also present in the Ashland material are specimens which agree in all respects with the description of *M. dubius* except that the thecae number 12 in 10 mm. in the proximal region of the rhabdosome.

MONOGRAPTUS FORBESI Berry, n. sp.
Text-figs. 2B,2G

Description.—The rhabdosome is long, slender and straight except for a slight ventral curvature in the proximal region which rarely involves more than the first six thecae. It has a maximum length of 6 cm. and widens gradually from an initial width of 0.3 mm. to a maximum of 1.2 to 1.4 mm.

The thecae number 8 to 9 in 10 mm. in the proximal region and 7 to 8 in 10 mm. in the distal. They are long and tubular, four to five times as long as they are wide, and overlap approximately one-half their length. They are inclined to the stipe at an angle of 13 to 17 degrees.

The sicula is small and slender. It is approximately 2 mm. long and 0.2 mm. wide; and its apex attains a level between that of the first and second thecal apertures.

Affinities.—This species resembles forms included in the *M. dubius* group in possessing a ventral curvature in the proximal region and in long, tubular, but unadorned thecae. It differs from species with which it might be confused on cursory examination such as *M. meneghini* Gortani and *M. praedubius* Boucek in number of thecae in 10 mm., in more slender thecae, and in a lesser angle of inclination of the thecae. The latter feature is the most diagnostic of this new species.

Holotype.—UCMP 37718.

MONOGRAPTUS TUMESCENS var. CONTUS
Berry, n. var.
Text-fig. 2C

Description.—The rhabdosome is 5 to 7 cm. long. It is straight distally, may have a slight dorsal curvature in the medial portion, and has a slight to strong ventral curvature in the proximal region. The ventral curvature involves the first four or five thecae. The rhabdosome widens rapidly from an initial width of 0.6 to 0.7 mm. to a maximum of 2.3 mm. The maximum breadth is attained at the tenth to twelfth theca and it is maintained thereafter except in a few specimens which narrow slightly in the distal extremity.

The thecae number 11 to 12 in 10 mm. in the proximal portion and 9 in 10 mm. in the distal. They are three to four times as long as they are wide, overlap two-thirds their length, and are inclined to the stipe at a 35 to 40 degree angle. The apertural margin is thickened and, upon compression, this commonly results in a distinct denticle. The proximal thecae are commonly shorter and slightly wider than those in the medial and distal portions of the rhabdosome.

The sicula is 1.5 mm. long and is four to five times as long as it is wide. Its apex attains the level of the second thecal aperture.

Affinities.—The variety *M. tumescens contus* is close to the typical *M. tumescens* Wood in size, shape, and thecal characteristics. It is longer and slightly wider than *M. tumescens sensu stricto* which is 2 to 4 cm. long and a maximum of 2 mm. wide. Also, the thecae number but 9 to 11 in 10 mm. in the typical form of *M. tumescens* and are inclined at an average of 30 degrees whereas in the variety *M. tumescens contus*, the thecae may number as many as 12 in 10 mm. and they are inclined at an average of 37 degrees. Further, the ventral curvature in the variety *M. tumescens contus* is less pronounced than in the typical form.

Holotype.—UCMP 37720.

MONOGRAPTUS VULGARIS var. ASHLANDENSIS Berry, n. var.
Text-fig. 2H

Description.—The rhabdosome is moderately long, 2.8 cm., and straight throughout its length. It widens gradually from 0.3 mm. initially to a maximum of 1.6 to 1.8 mm. The thecae number 9 in 10 mm. in the distal portion and 11 to 12 in 10 mm. in the proximal. They are straight and tubular, are three times as long as they are wide, overlap approximately one-half their length, and are inclined to the stipe at an angle of 35 to 43 degrees. The thecal apertures appear to have a thickened margin.

The sicula is approximately 1.2 to 1.3 mm. long and is four times as long as it is wide. It reaches to the level of the second thecal aperture.

Affinities.—This form is characterized by its stiff, completely straight shape, as is *M. vulgaris* Wood. It also resembles the typical form of *M. vulgaris* in number of thecae, and in inclination of the thecae. *M. vulgaris*, however, is 5 to 10 cm. long and 2.5 mm. wide. This new variety is shorter and narrower. Also, its distal thecae are somewhat shorter and narrower, being three times as long as they are wide compared to four times the width in mature thecae of *M. vulgaris sensu stricto*. This new variety is also similar to *Pristiograptus spectatus* Pribyl in shape and dimensions except that that species is slightly wider (0.6 to 0.7 mm.) initially. The proximal region of *P. spectatus* commonly has a slight ventral curvature and the first two thecae in *P. spectatus* have slight ogee curvature of their ventral walls.

Holotype.—UCMP 37721.

MONOGRAPTUS sp.
Text-fig. 2D

One poorly preserved specimen may be described as follows: The rhabdosome is at least 3.5 mm. long and widens from 0.4 mm. initially to 1.4 to 1.5 mm., then remains that width throughout its length. It has a marked ventral curvature in the proximal region which involves the first 12 to 14 thecae.

The thecae number 7 in the first 5 mm. and then become less closely spaced—numbering 10 in 10 mm. in the distal part. The ventral walls of the thecae appear to be distinctly curved. Some are almost glyptograptoid in aspect. The thecal apertures of the proximal thecae are situated in distinct excavations, whereas the apertures of the distal thecae are nearly horizontal. This unique thecal appearance may be a factor of preservation and not their original shape. The specimen is not well enough preserved to be sure.

The sicula is approximately 2 mm. long and 0.3 mm. wide. Its apex nearly attains the level of the second thecal aperture.

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FORAMINIFERAL BIOFACIES OFF THE SOUTH CHINA COAST

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ABSTRACT—About 147 bottom samples from the Asiatic Shelf, south of Taiwan Island and in the Gulf of Tonkin were analyzed for their foraminiferal content. It was found that the foraminiferal number, percentage of planktonic Foraminifera and species number increased with depth. The occurrence of high percentage areas of arenaceous and porcelaneous populations were bimodal, parallel to shore. No unidirectional trends were noted with the hyaline population. Glauconite replacement of Foraminifera was most pronounced in Hainan Strait.

Four depth dominant faunas were established:

Inner Shelf Fauna (65–150 feet) *Elphidium advenum, E. sagrum, Nonion japonius*
Central Shelf Fauna (151–275 feet) *Amphistegina lessonii, Hanzawaia nipponica, Streblus tepidus*
Outer Shelf Fauna (276–400 feet) *Biloculinella labiata, Cassidulina neocarinata, Spiroloculina communis*
Upper Bathyal Fauna (401–656 feet) *Bolivina spathylata, Uvigerina auberiana, U. schwageri*

INTRODUCTION

GENERAL

ANCIENT shelf deposits have long been of interest to the oil industry as potential petroleum reservoirs. This study investigates the ecology of the Foraminifera of the Asiatic Shelf (Text-fig. 1) in an effort to establish some parameters for recognizing and understanding similar environments in the geologic column.

This study was made at the University of Southern California during the summer and fall of 1957 and spring of 1958 as partial fulfillment of requirements for a Master's degree. Samples were supplied by Dr. Hiroshi H. Niino, of the Tokyo University of Fisheries. Dr. Niino and Dr. K. O. Emery examined the sedimentologic properties of these and other samples in a joint study at the University of Southern California in 1956 and 1957. All of the 1000 small snapper samples, of which about 14 were used in this study, were collected by Japanese boats since 1920. All but two of the samples are between 20 meters (65 feet) and 200 meters (656 feet). No preserving agent was added to the samples when collected.

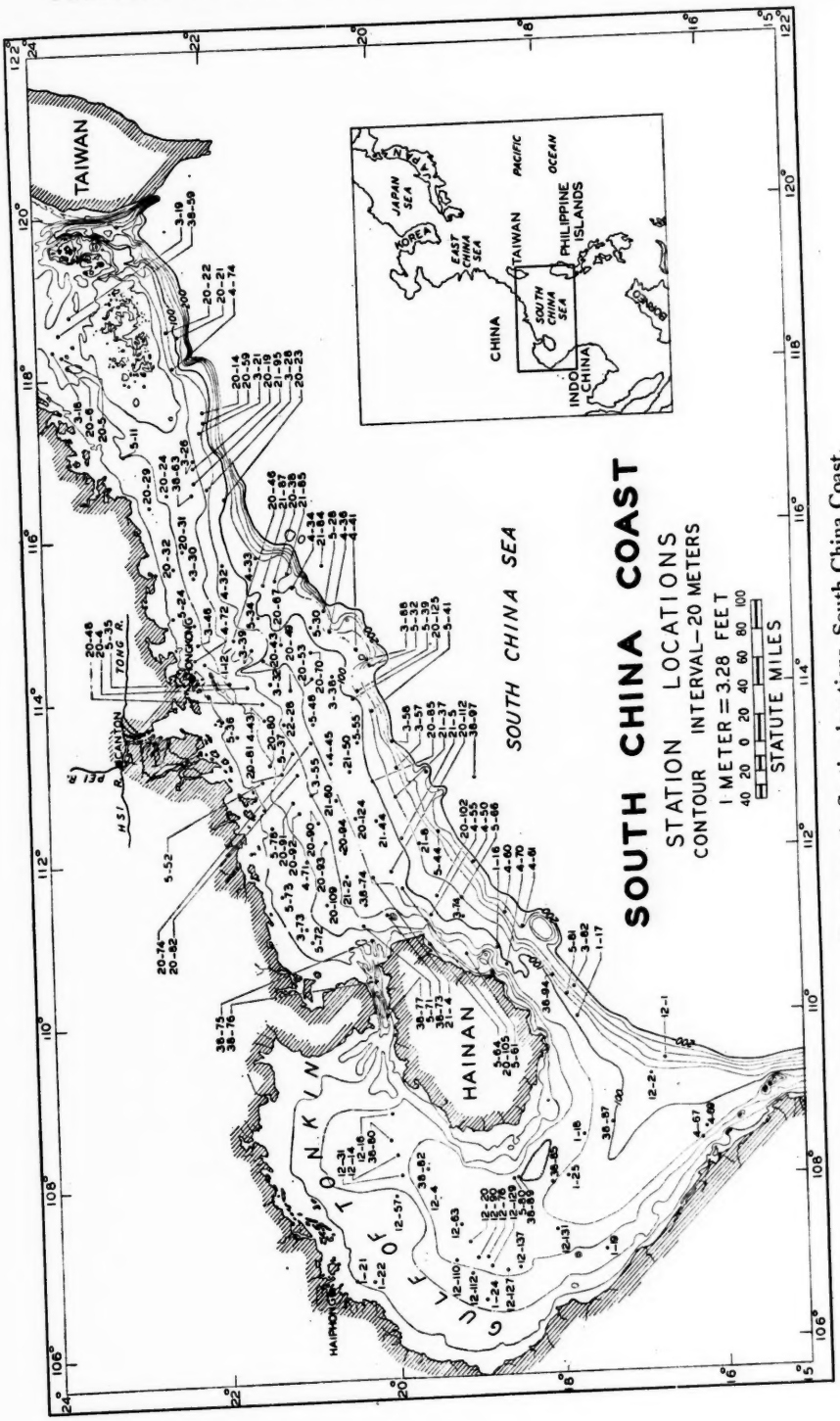
METHOD OF STUDY

The dry samples were weighed and washed on 250-mesh Tyler screens (0.061-mm. openings). About 300 specimens were counted from each sample when possible. Samples having fewer than 100 specimens were not used.

Table I is a list of four benthonic species with comparisons to previous reports with depth information. Table II lists cumulative percentages of dominant faunas.

PREVIOUS WORK

There have been no previous studies of the foraminiferal ecology of the southern Asiatic Shelf. Cushman reported on some Foraminifera from the North Pacific Ocean (1910–17) and from the Philippine Sea and Asiatic Shelf (1921) giving some bottom temperatures. Hada (1929, 1931, 1936, 1937, 1943, 1943) studied the Recent Foraminifera in local areas around Japan and the South Pacific with some ecological interpretations. Oinomikado & Stach (1948) investigated some Recent shallow water assemblages from the Niigata Prefecture of Japan. Asano (1950) presented a taxonomic paper on the Japanese Tertiary Foraminifera and later (1956, 1957, and 1958) reported upon some Nodosariidae, Miliolidae and Buliminidae from the sea around Japan. This work includes information on bottom temperature, depth and character of the bottom. Saidova (1957) examined the Foraminifera in the deep sediments of the Okhotsk Sea. Data on depth, temperature and salinity were included.



TEXT-FIG. 1—Station locations, South China Coast.

TABLE 1—FOUR BENTHONIC SPECIES WITH COMPARISONS TO PREVIOUS REPORTS OF DEPTH INFORMATION

	Depth in Feet	
	Asiatic Shelf	Other
Cassidulina neocarinata	203–597	394– 1,940 (Parker, 1954)
Bulimina marginata	65–590	246– 1,050 (Parker, 1954)
Gyroidina soldanii rotundimargo	230–508	2,200– 2,900 (Natland, 1933)
Uvigerina auberiana	230–597	739–10,620 (Parker, 1954)

ACKNOWLEDGMENTS

The writer is especially indebted to Orville Bandy for suggesting the study and for his invaluable assistance and criticisms. K. O. Emery offered aid and suggestions throughout the investigation, and William H. Easton reviewed the thesis manuscript. Hiroshi H. Niino very generously supplied the samples. Thanks are due to Miss Ruth Todd of the U. S. National Museum for comparing specimens of *Cibicides haidingeri pacificus* with the holotype. I am grateful to the Allan Hancock Foundation for the use of the laboratories and library. The assistance of F. P. Shepard of the Scripps Institute of Oceanography is appreciated for making available to me temperature, salinity and density data.

This study is a contribution of the Allan Hancock Foundation, University of Southern California, Los Angeles, California.

OCEANOGRAPHY

CURRENTS

The main Kuroshio Current flows in a northeast direction, around both sides of Taiwan Island, crosses the break in slope and travels over the shelf to Korea where it is deflected into the Yellow and Japan Seas. This current is a high temperature, high salinity water mass. It is broadest and strongest in the summer when branches of it extend into the Gulf of Tonkin. Its effective depth is approximately 700 meters (Sverdrup, 1946).

A low temperature, low salinity countercurrent flows southward along the coast. Large rivers contribute to this current, which is most strongly defined in the winter.

SALINITY

Surface salinity increases with distance from shore and has values of 34 parts per thousand near the outer edge of the continental shelf. In summer, when the Hsi River is in flood, salinities off Hong Kong drop to 27 parts per thousand. This small variation is due to the low volume of fresh water inflow from rivers.

Yearly averages of bottom salinity vary from 32 parts per thousand near the mainland to 34 parts per thousand at the break in slope and far into the Gulf of Tonkin (Text-fig. 2).

TEMPERATURE

Summer surface isotherms (27°C. to 30°C.) curve back and forth gently throughout the area, whereas winter isotherms (15°C. to 22°C.) lie parallel with the coast.

Average yearly bottom temperatures range from 25°C. in 25 to 150 feet of water to approximately 10°C. just beyond the break in slope (Text-fig. 3).

BOTTOM TOPOGRAPHY

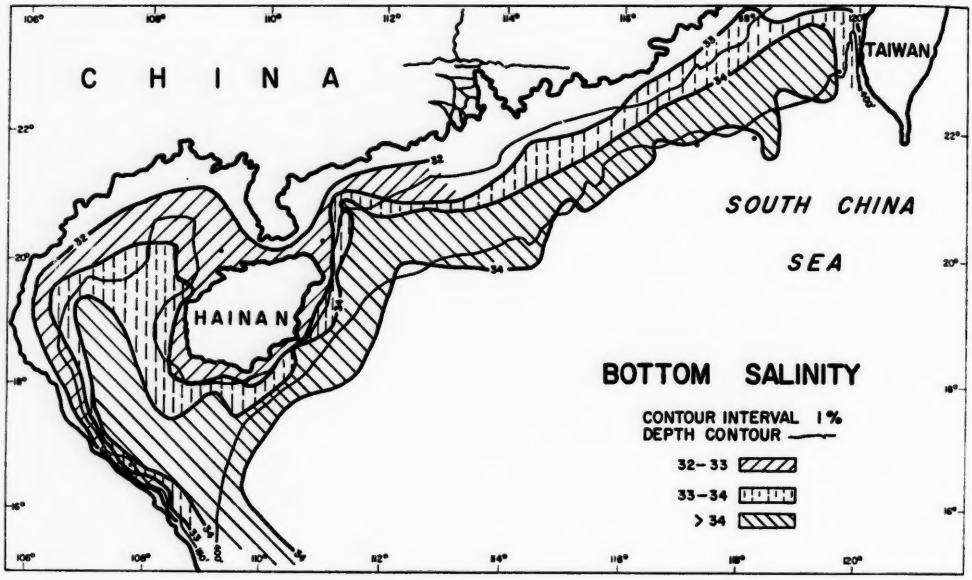
For 725 miles, from Taiwan Strait southwestward to French Indo China, a broad (80 to 300 miles) gently sloping continental shelf underlies the south China Sea and the Gulf of Tonkin (Text-fig. 1). The break in slope occurs at approximately 122 meters (400 feet). From Taiwan Strait to Hainan Island, with the exception of the Pescadores Islands, no basins, canyons or seamounts interrupt the smooth sea floor.

The Gulf of Tonkin extends about 300 miles from head to mouth. It has a smooth flat floor except for irregularities in Hainan Strait where bottom currents have scoured a depression about 16 feet below the sea floor at either end. Tidal deltas have formed at each end of Hainan Strait.

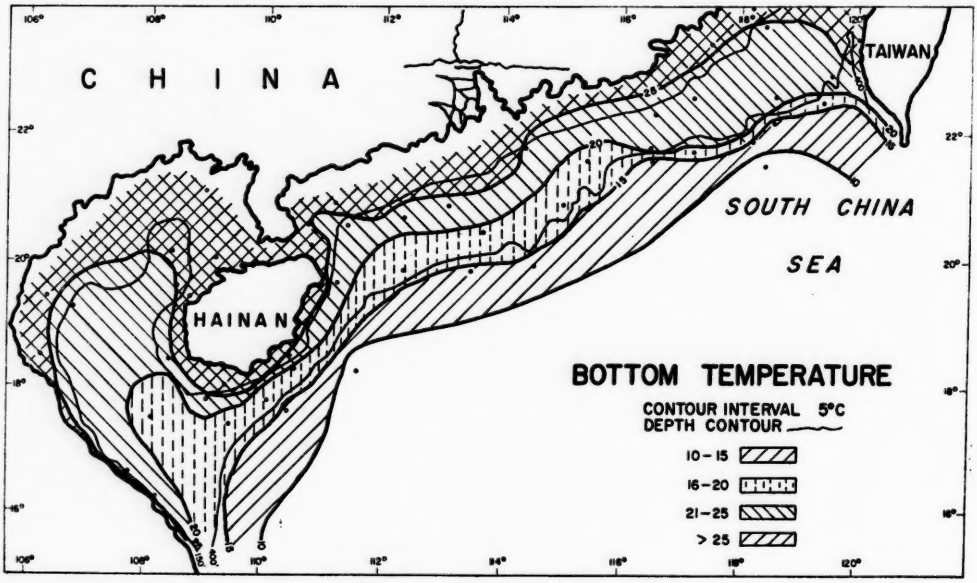
Niino & Emery (1957) estimate the size of the continental shelf from Taiwan Strait to Hainan Island to be about 300,000 square kilometers and the Gulf of Tonkin to be approximately 170,000 square kilometers.

TABLE 2—CUMULATIVE PERCENTAGES OF DOMINANT FAUNAS

	Inner Shelf	Central Shelf	Outer Shelf	Upper Bathyal
	Depth in Feet			
	54–150	151–275	276–400	401–660+
INNER SHELF FAUNA				
Ammobaculites agglutinans	0.3	0.0	0.0	0.0
Elphidium advenum	3.0	1.4	0.5	0.0
E. panamense	0.3	0.0	0.0	0.0
E. sagrum	4.0	0.7	0.4	0.0
Guttulina problema indica	0.4	0.1	0.02	0.0
Nonion japonicus	6.1	5.0	1.5	0.1
Quinqueloculina agglutinata	0.5	0.25	0.14	0.3
Q. boueana	0.75	0.0	0.04	0.0
Spiroloculina valida	0.2	0.0	0.0	0.0
Streblus beccarii annectens	0.5	0.3	0.03	0.0
Totals	16.05	7.75	2.63	0.4
CENTRAL SHELF FAUNA				
Amphistegina lessonii	1.1	9.8	2.6	1.7
Elphidium craticulatum	2.0	4.1	2.2	0.8
Glandulina elliptica	0.2	0.3	0.1	0.0
Hawzawaia nipponica	6.2	7.6	2.8	1.5
Lagena pliocenica	0.0	0.2	0.1	0.0
Loxostomum mayori	1.4	5.2	2.3	0.0
Operculina bartschi ornata	1.8	2.1	1.23	0.5
Poroeponides cribrorepandus	1.3	2.0	0.54	0.0
Quinqueloculina disparilis curta	0.0	0.2	0.14	0.0
Q. kerimbatica philippeninsis	0.1	0.4	0.1	0.0
Sigmoilina amygdaloides	0.3	0.5	0.2	0.1
Streblus tepidus	4.4	6.0	1.8	0.6
Totals	18.8	38.4	14.11	5.2
OUTER SHELF FAUNA				
Biloculinella labiata	0.0	0.0	1.35	0.2
Cancris oblongus	0.2	0.3	0.6	1.0
Cassidulina neocarinata	0.1	0.4	1.6	2.9
Cibicides lobatulus	0.0	0.2	0.5	0.0
C. margaritiferus	0.0	0.1	0.73	0.8
Dentalina vertebralis	0.4	0.2	0.4	0.0
Epistominella pulchra	0.1	1.0	1.1	1.1
Gaudryina wrightiana	0.0	0.3	0.3	0.0
Neorotalia ozawai	0.4	0.0	0.7	0.0
Nonion grateloupi	0.0	0.0	0.1	0.0
Quinqueloculina sagmiensis	0.3	0.2	0.8	0.0
Reussella haizumensis	0.3	0.5	0.5	0.0
Scutuloris oblongus	0.1	0.0	0.43	0.0
Robulus expansus planulatus	0.0	0.0	0.15	0.0
Spirolina acicularis	0.0	0.0	0.05	0.0
Spiroloculina communis	0.9	1.0	1.88	2.8
Streblus trispinosus	0.0	0.0	0.1	0.0
Totals	2.8	4.2	11.29	8.8
UPPER BATHYAL FAUNA				
Bolivina spathulata	1.7	2.2	1.6	5.6
Cassidulina subglobosa	0.0	0.0	0.12	1.2
Fissurina marginata	0.5	0.8	0.5	1.8
Höglundina elegans	0.1	0.3	0.5	1.2
Operculina gaymardi	0.1	0.5	0.6	1.2
Uvigerina auberiana	0.3	0.0	2.0	3.1
U. schwageri	0.1	0.0	0.6	2.9
Totals	2.8	3.8	5.92	17.0



TEXT-FIG. *2*—Bottom salinity.



TEXT-FIG. *3*—Bottom temperature.

GENERAL FAUNAL CHARACTERISTICS

FORAMINIFERAL NUMBER

The foraminiferal number represents the total number of foraminiferal tests per gram dry weight of unwashed sample (Foraminifera/gm.). Planktonic forms are included.

In general, the foraminiferal number increases with depth to the break in slope at 400 feet, somewhat beyond which it decreases (Text-fig. 4). A similar increase in values to beyond the break in slope was reported by Bandy & Arnal (1957). A belt of values ranging from 1000 to 4000 Foraminifera/gm. is found on the Outer Shelf (276–400 feet). Within this belt are two highs of 8000 and 25,200 Foraminifera/gm. Just beyond the break in slope one sample has 10,100 Foraminifera/gm. Values of fewer than 100 Foraminifera/gm. are found in the Gulf of Tonkin on the Inner Shelf (65–150 feet) and directly out from the Hsi River estuary to the break in slope.

Low values off the Hsi River estuary can be attributed to the debouching fresh river water, which is not conducive to the proliferation of Foraminifera, and the rapid sedimentation which dilutes the concentration of foraminiferal tests. Highest values in the Gulf of Tonkin follow the inflowing plankton-rich, oceanic water of the Kuroshio Current.

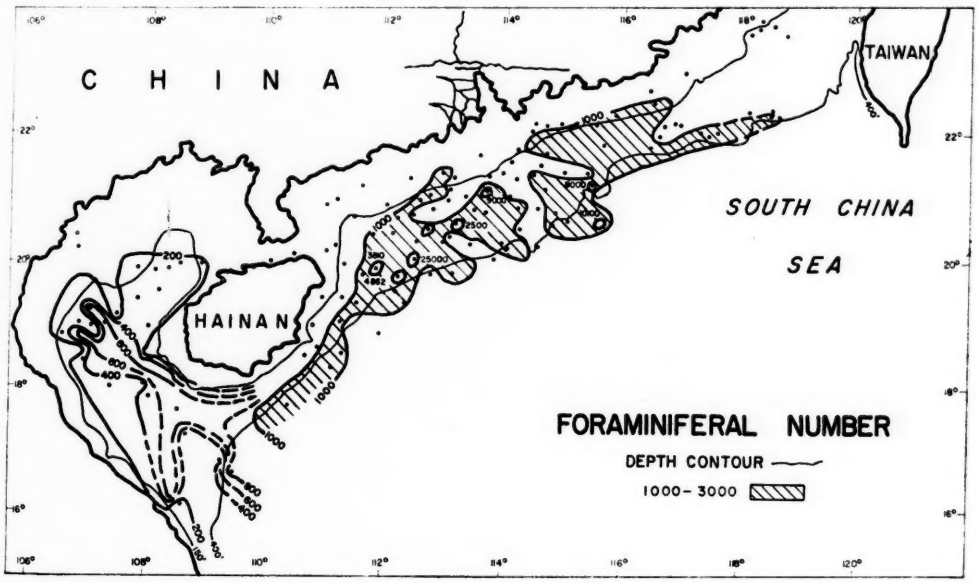
PLANKTONIC FORAMINIFERA

The planktonic population is measured as a percentage of the entire population and is considered ecologically distinct from the benthonic Foraminifera.

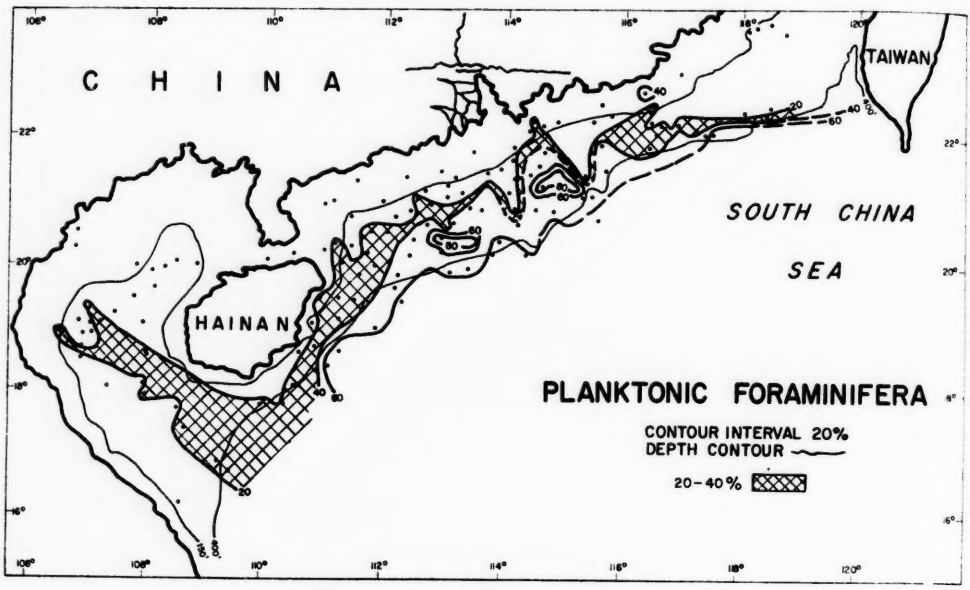
There is an increase with depth in the percentage of planktonic Foraminifera (Text-fig. 5). Highest percentages observed were on the Outer Shelf in two areas that straddle low percentage areas off the Hsi River estuary. A similar situation exists with the foraminiferal number, indicating the presence of nutrient-rich areas and that the foraminiferal number directly reflects the distribution of the planktonic population. This is borne out by like trends in the Gulf of Tonkin.

BENTHONIC FORAMINIFERA—ARENACEOUS

The arenaceous population exhibits bimodal occurrence of high percentage areas (more than 10 percent) in bands running



TEXT-FIG. 4—Foraminiferal number (specimen per gram of dry sediment).



TEXT-FIG. 5—Planktonic Foraminifera.

parallel to the shoreline (Text-fig. 6). Percentages of more than 20 are found between depths of 130 and 260 feet off large river mouths and on the shelf side of the Hainan Strait. These high percentages can be attributed to four widespread species: *Clavulina yabei akiensis*, *Goesella rotundata*, *Spiroplectammina floridana*, and *Textularia candeiana*.

BENTHONIC FORAMINIFERA—PORCELANEOUS

Bands of high percentages parallel to the coast separated by areas of low occurrence depict the distribution of the porcelaneous population on the shelf and in the Gulf of Tonkin (Text-fig. 7). High values in Taiwan Strait, set apart from other high occurrence areas infer a different faunal province. A similar phenomenon was detected with the arenaceous population. No unidirectional trends are apparent.

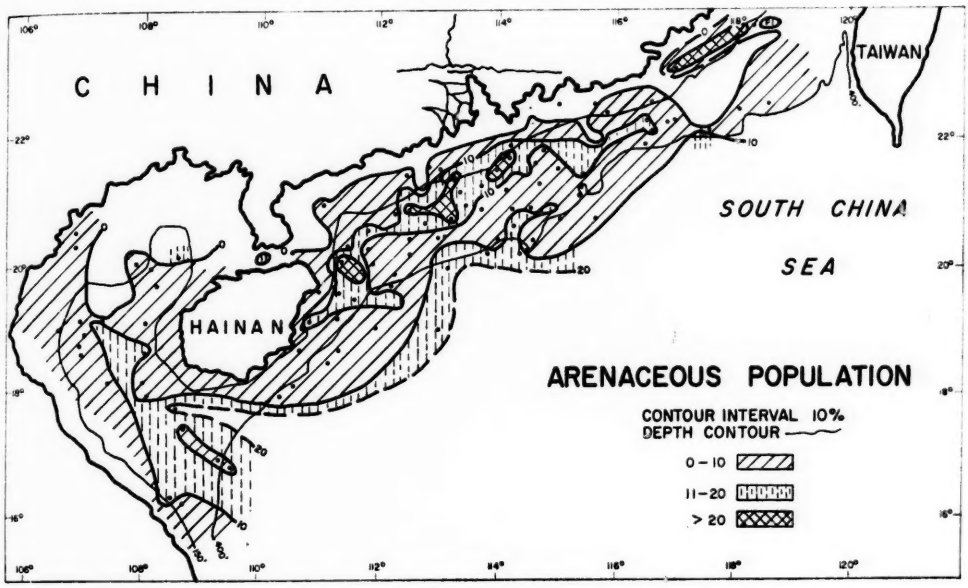
Inshore abundances could not be observed here because no samples were available shallower than 65 feet. Zero percentages line up at the shallowest stations on the shelf and into the Gulf of Tonkin. This area is alternately occupied by low temperature, low salinity countercurrents in the winter and high temperature, high salinity Kuroshio Current water in the summer. The porcelaneous population ranges extensively on the shelf, both in areal and depth distribution.

BENTHONIC FORAMINIFERA—HYALINE

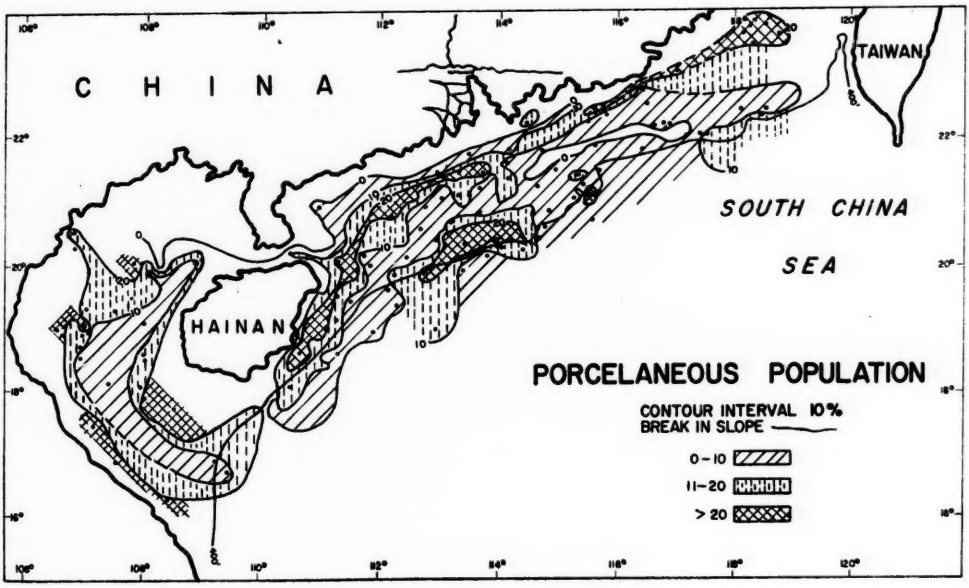
Abundant hyaline Foraminifera occur northeast of the Hsi River estuary along the break in slope and coastline. Lower percentages exist in the central and Outer Shelf.

Cold, surface, coastal countercurrents moving across the Hsi River estuary cover large areas of high percentage. The same effect is found in the Gulf of Tonkin. Because bottom water temperature contours fail to show this trend, it seems reasonable to assume that surface currents can affect the distribution of benthonic Foraminifera.

Amphistegina lessonii occurs in quantities greater than 50 per cent in a marly matrix, often with *Operculina bartschi ornata*, near Taiwan Strait in 170 to 190 feet of water. Bandy (1954) referred the occurrence of *Amphistegina lessonii* in the Gulf of Mexico to a fossil algal belt between depths of 130 to 350 feet. Localized occurrence of such an



TEXT-FIG. *6*—Arenaceous Foraminifera.



TEXT-FIG. *7*—Porcelaneous Foraminifera.

area, together with some chalky specimens, suggest at least a sub-Recent dating or a fossil reef.

Neorotalia ozawai is found in percentages of 52 and 16 at depths of 230 and 330 feet just south of the Taiwan Strait. Most of these specimens have a chalky appearance. It is not certain whether this species is fossil, since it is found at two other stations on the shelf and one in the Gulf of Tonkin.

Hainan Strait yields 33 and 25 percent abundances of *Poreoponides cribrorepandus* at depths of 128 and 193 feet. Here again, chalky specimens indicate fossil outcrops of sub-Recent material. Asano (1950) first described this species from the Pliocene of Japan. Because of the bottom scouring currents in this strait, as reported by Niino & Emery (1957), the fossil outcrop interpretation is preferred. Replaced Foraminifera make up the balance of the fauna here.

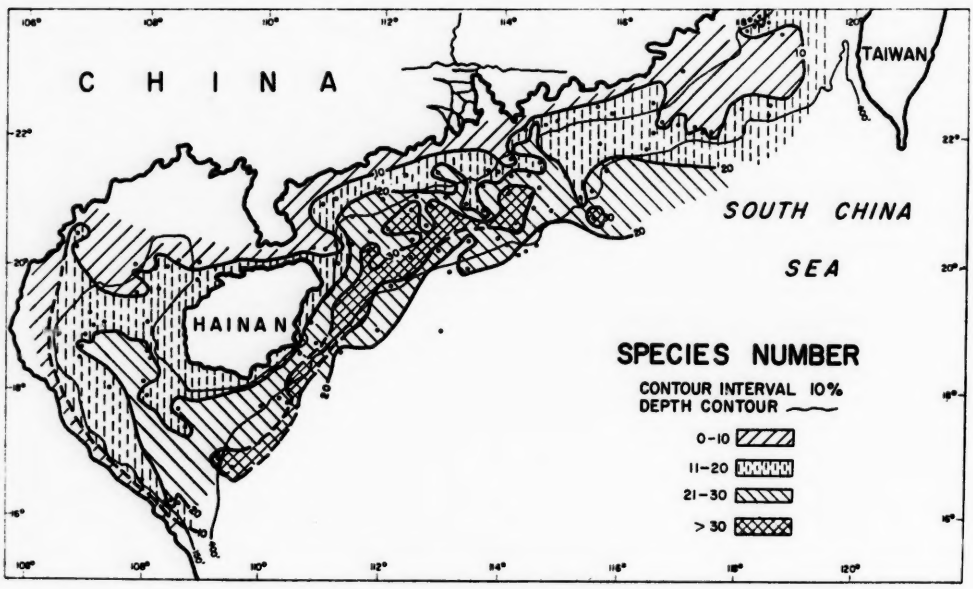
Of the Recent species previously reported with depth information, only *Cassidulina subglobosa* was found deeper on the Asiatic Shelf. Only four species occur shallower than previously reported (Table I). Parker (1954) reported on the Gulf of Mexico, which has a broad shelf. The discrepancies here are not as great as with Natland (1933) who found *Gyroidina soldanii rotundimargo* in 2200 to 2900 feet of water in the San Pedro Basin off California, where the shelf is narrow. Distance from shore may be a controlling factor. Progressing away from shore, turbidity, and particulate matter in the water decrease. Perhaps foraminiferal distribution is controlled, in part, by what suspended material in the water reaches the bottom and the declivity of the sea floor which could cause displacement.

SPECIES NUMBER

The number of species per sample constitutes the species number. Conditions favoring speciation are presumed to exist where the highest species numbers are found. Exactly which conditions cause speciation are not known. Bandy & Arnal (1957) reported an increase in the number of species "away from shore into a progressively more stable environment." An increase in the species number is noted away from shore off the south China coast (Text-fig. 8).

FAUNAL ANALYSIS

Faunal analysis was made using composite frequency distribution of benthonic Foraminifera plotted against cumulative



TEXT-FIG. 8—Species number.

percentage, with stations grouped according to depth (Text-fig. 9). This method of analysis shows gross trends whereas localized high percentages may not be detected. Bottom temperatures and salinities are included below.

Four dominant faunas are apparent: Inner Shelf fauna from 65 to 150 feet; Central Shelf fauna from 151 to 275 feet; Outer Shelf fauna from 276 to 400 feet; Upper Bathyal fauna from 401 to 656 feet.

Inner Shelf Fauna—65 to 150 feet (Table II) (Text-fig. 10)
Temperature more than 25°C.
Salinity less than 33 parts per thousand.

The genus *Elphidium* dominates the Inner Shelf fauna, represented by *Elphidium advenum*, *Elphidium panamense* and *Elphidium sagrum*. *Nonion japonicus* is more abundant than the three *Elphidium* spp., but is widespread on the Central Shelf. Bandy (1956) found *E. advenum* and *Quinqueloculina agglutinata* well within the 150 foot depth. Percentages greater than 10 are contained inside the 150 foot contour except off the Hsi River estuary. River waters would seem to be responsible for this.

Kuroshio Current patterns of movement are well defined by areas of zero percentage, especially in the Gulf of Tonkin and Hainan Strait. It seems that surface currents here affect the benthonic fauna.

Central Shelf Fauna—151 to 275 feet (Table II) (Text-fig. 11)
Temperature more than 23°C.
Salinity less than 34 parts per thousand.

This fauna is more abundant and widespread than the Inner Shelf fauna. Due to its high percentages in areas deeper than 150 feet, *Streblus tepidus* is placed in the Central Shelf fauna. Some chalky and broken specimens of *Amphistegina lessonii* indicate possible fossil outcrops. Many specimens of *Elphidium craticulatum*, *Hanzawaia nipponica* and *Loxostomum mayori* were well preserved and may be better depth indices for this zone.

Outer Shelf Fauna—276 to 400 feet (Table II) (Text-fig. 12).
Temperature from 15°C. to 20°C.
Salinity greater than 33 parts per thousand.

Strong shelf affinities are displayed by this cosmopolitan, widespread fauna. Percentages from 10 to 60 occur consistently between the 150 foot and 400 foot contours.

Biloculinella labiata, *Cassidulina neocarinata* and *Spiroloculina communis* dominate this depth interval. Although the latter two species have higher percentages in the Upper Bathyal zone they are placed in this fauna because of their extensive distribution between 276 and 400 feet and the possibility of their being concentrated by displacement downslope.

Poroeponides cribrorepandus, although believed to be fossil in Hainan Strait, is listed as an Outer Shelf species because it comprises more than three percent of the fauna found in ten widely dispersed samples in appropriate water depths.

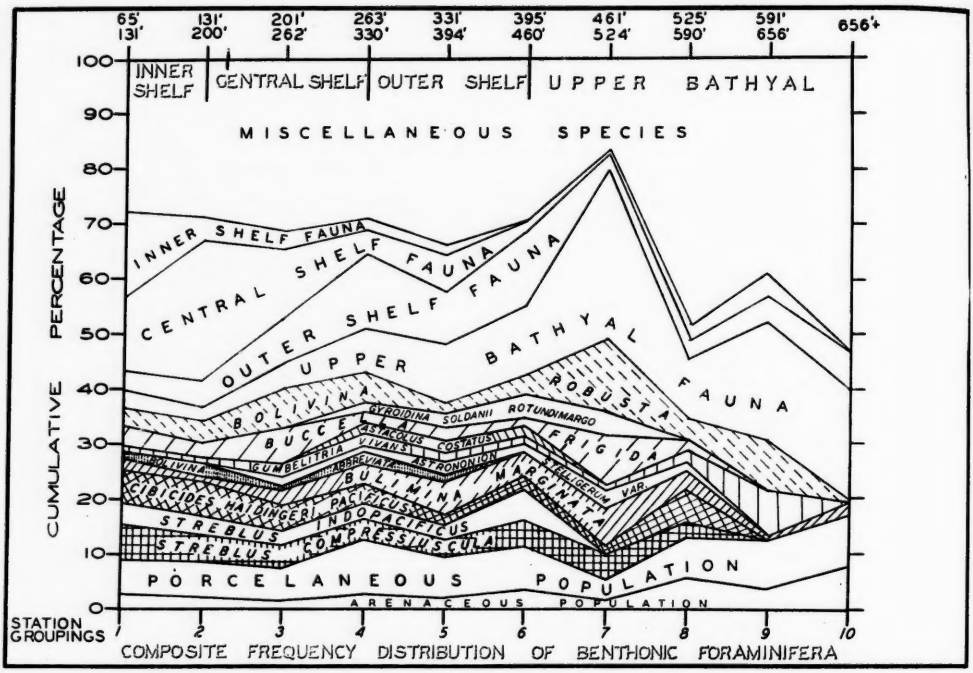
Neorotalia ozawai, like *Poroeponides cribrorepandus*, may be living and fossil. They are most abundant between 151 and 400 feet.

Upper Bathyal Fauna—401 to 656 feet (Table II) (Text-fig. 13)
Temperature from 10°C. to 15°C.
Salinity 34 parts per thousand.

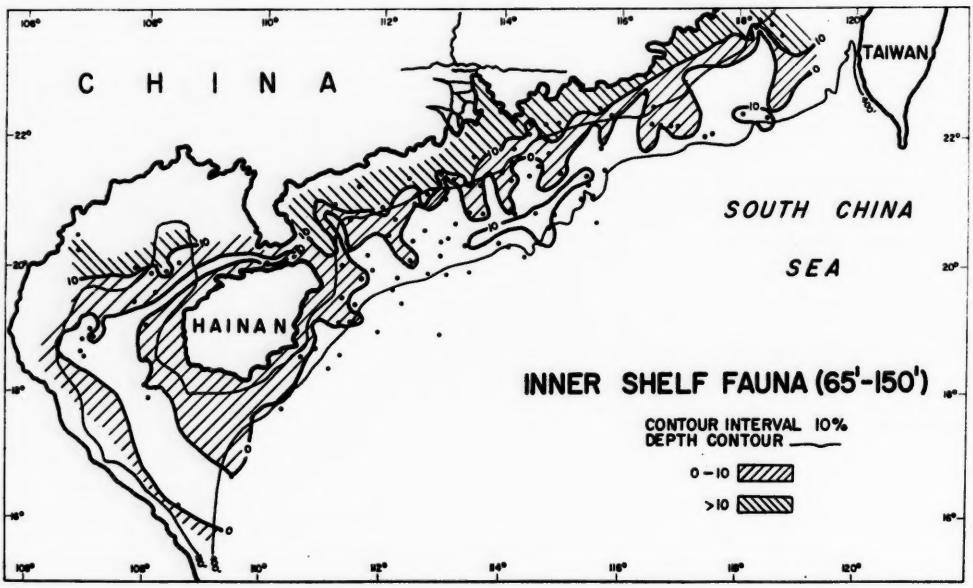
Bolivina spathulata, *Uvigerina auberiana* and *U. schwageri* are the most common Foraminifera found in this depth range. Southwest of the Hsi River estuary this fauna reveals percentages greater than 20 undulating across the break in slope, then is abruptly swept far upslope into the Gulf of Tonkin. It could be that the Kuroshio Current sweeps this fauna upslope, or that distance from shore is the controlling factor. The Kuroshio Current may so dilute the coastal waters in the Gulf of Tonkin as to produce that critical nutrient value that is conducive to the proliferation of the Upper Bathyal fauna. Different values may exist for each fauna or species, the distribution of which would be controlled by nutrient supply, which in turn could be a function of distance from shore and the diluting action of oceanic waters.

Parker (1948), Colom (1950), and Natland (1933) reported *Hoglundina elegans* from Upper Bathyal depths. Bandy (1953) and Walton (1955) reported it from greater than 8000 feet and 2400 feet, respectively. The last two significantly were from narrow shelves.

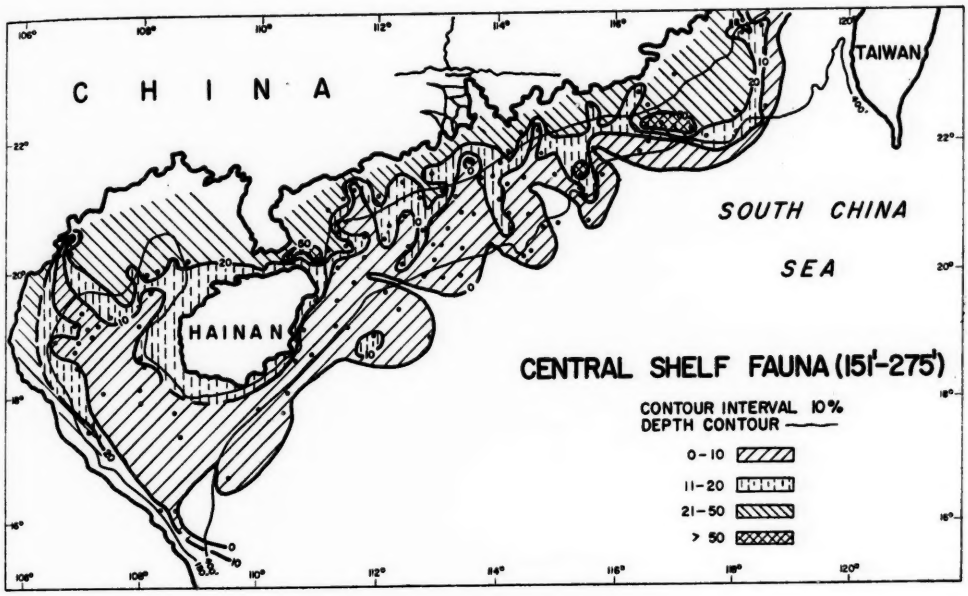
Uvigerina auberiana was reported by Parker (1954) from 739 to 10,670 feet, con-



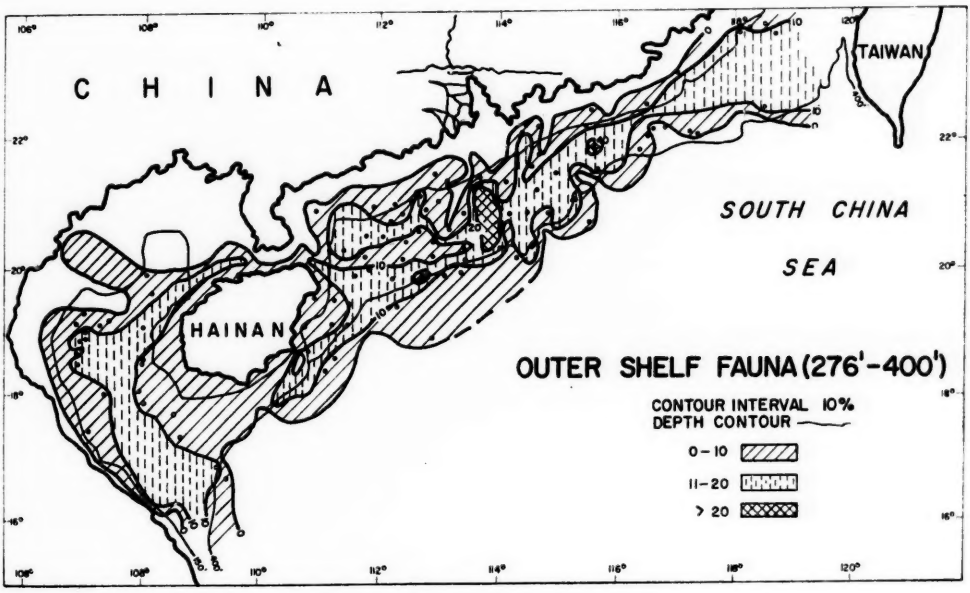
TEXT-FIG. *9*—Composite frequency distribution of benthonic Foraminifera.



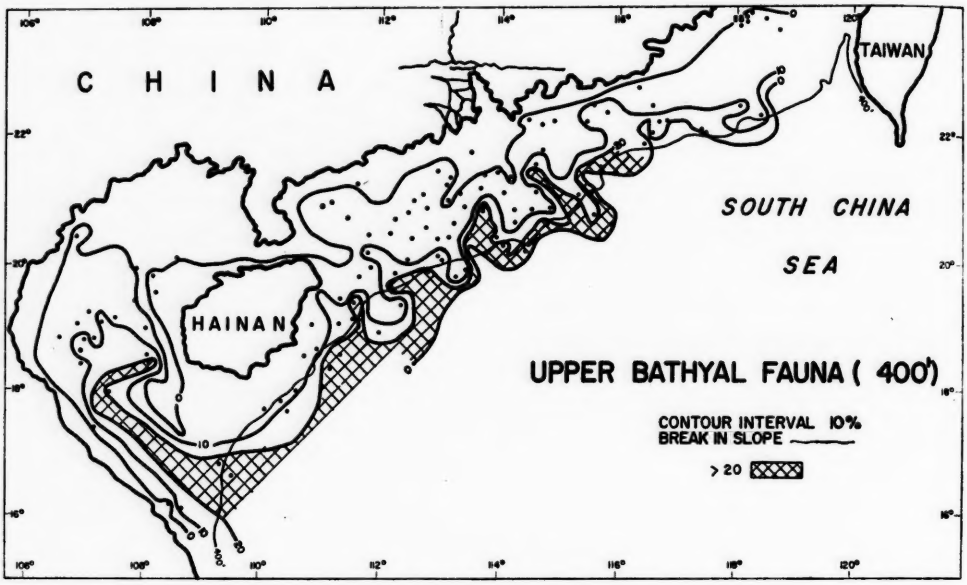
TEXT-FIG. *10*—Inner shelf fauna.



TEXT-FIG. *11*—Central shelf fauna.



TEXT-FIG. *12*—Outer shelf fauna.



TEXT-FIG. *13*—Upper bathyal fauna.

siderably deeper than the deepest sample here. Its upper limit here is higher, perhaps due to the broadness of the Asiatic Shelf.

WELL PRESERVED FORAMINIFERA

Inasmuch as none of the samples was stained, the state of preservation was the only criterion that seemed reasonable to use in determining which specimens represented the living population. Some fossil Foraminifera occur in an excellent state of preservation, and for this reason the term "well preserved" is used rather than "living." Clear, glassy, unfilled, unbroken tests constituted recognition of well preserved Foraminifera. Chalky, filled or broken tests were considered fossil. Only hyaline Foraminifera were so determined.

The mid-shelf area of current mixing defines this high percentage distribution of well preserved Foraminifera (Text-fig. 14). Warm bottom water zones (greater than 25°C.) north and west of Hainan Island correspond to zero percentage contours.

The most widely distributed species in this category are:

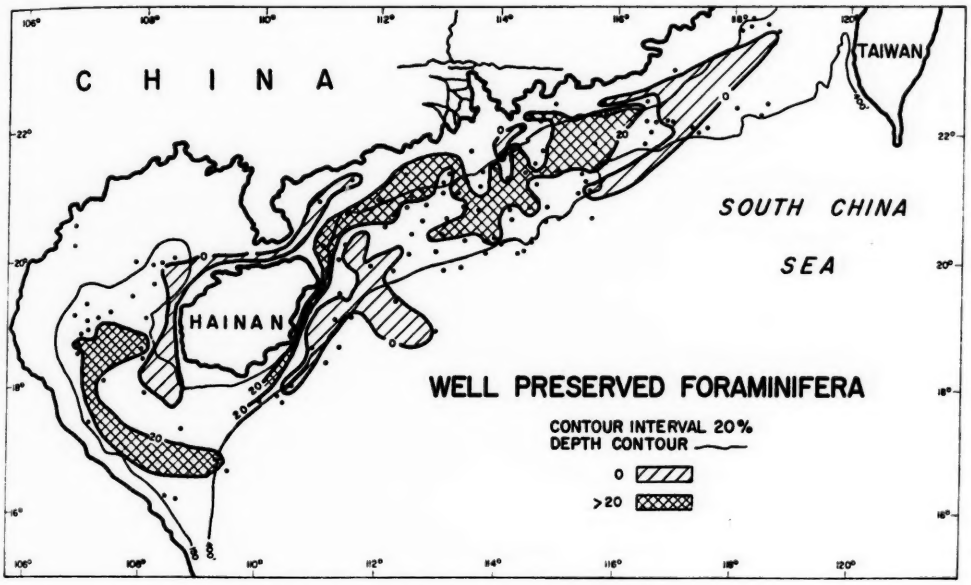
Cassidulina neocarinata
Fissurina marginata
Gumbelitria vivans (for discussion of this species, see Polski & Waller, 1958)

The balance of the well preserved fauna is:

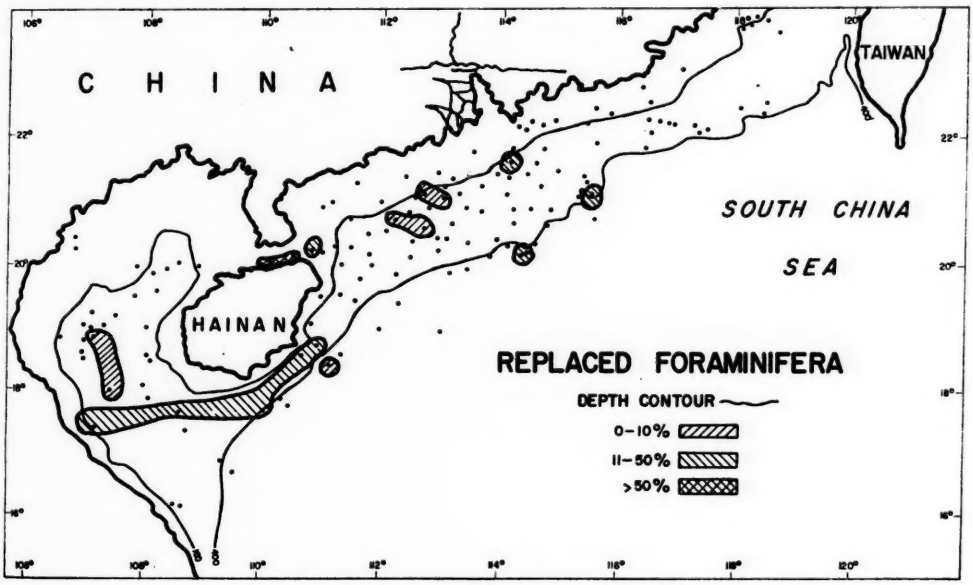
Astacolus tricarinellus
Astrononion stelligerus var.
Bolivina abbreviata
B. spathulata
Bucella frigida
Cancris sagra
Cibicides lobatulus
Elphidium advenum
Epistominella pulchra
Glandulina elliptica
Hanzawaia nipponica
Lagenonodosaria scalaris separans
Lagena sulcata spicata
Nonion japonicus
Operculina bartschi ornata
O. gaymardi
Virgulina schreibersiana

REPLACED FORAMINIFERA

Glauconite replaces test material of many benthonic and a few planktonic Foraminifera. Highest percentages (over 50) of replaced Foraminifera were found in the Hainan Strait (Text-fig. 15). Here, bottom-scouring waters have excavated some fossil material, at least preventing deposition. Replacement occurs mostly with benthonic forms, although a considerable number of specimens of the genus *Globigerina* were replaced.



TEXT-FIG. *14*—Well preserved Foraminifera.



TEXT-FIG. *15*—Replaced Foraminifera.

CONCLUSIONS

1. Foraminiferal number increases with depth, reaching highest values on the Outer Shelf, and decreasing somewhat beyond the break in slope.

2. Planktonic Foraminifera increase in abundance with depth.

3. Pronounced sudden decrease in the percentage of planktonic Foraminifera can be attributed to debouching river water and can indicate ancient river mouths in fossil sediments.

4. Bimodal occurrence in bands of high values paralleling the coast describes the distribution of the arenaceous and porcelaneous populations.

5. *Textularia candeiana, Goessella rotundata, Spiroplectammina pseudocarinata* and *Clauvulina yabei akiensis* are most abundant and widespread arenaceous Foraminifera and are good shelf indicators.

6. Porcelaneous Foraminifera increase toward shore in the Gulf of Tonkin which has no yearly current direction change.

7. A variety of porcelaneous forms indicates shelf conditions.

8. Highest percentages of hyaline Foraminifera occur off the Hsi River estuary.

9. Fossil specimens of *Amphistegina lessonii, Neorotalia ozawai* and *Poroeponides cribrorepandus* were found in localized areas.

10. Well preserved Foraminifera are most abundant at Inner and Central Shelf depths.

11. *Cassidulina neocarinata, Fissurina marginata* and *Gumbelitria vivans* are widely distributed species that consistently appear well preserved and are assumed to be living.

12. Four dominant faunas are evident:

Inner Shelf (65–150 feet)
Elphidium advenum
E. sagrum
Nonion japonicus
Central Shelf (151–275 feet)
Amphistegina lessonii
Hanzawaia nipponica
Streblus tepidus
Outer Shelf (276–400 feet)
Biloculinella labiata
Cassidulina neocarinata
Spiroloculina communis
Upper Bathyal (401–656 feet)
Bolivina spathulata
Uvigerina auberiana
U. schwageri

13. Species number increases with depth to the break in slope, with maximum values on the Outer Shelf.

14. Glauconite replacement of planktonic and benthonic Foraminifera is widespread on the shelf, but most pronounced in Hainan Strait.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 6, P. 1183–1197, 3 TEXT-FIGS., NOVEMBER, 1960

A PALEOECOLOGIC STUDY OF THE UPPER DENTON FORMATION, TARRANT, DENTON, AND COOKE COUNTIES, TEXAS

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ABSTRACT—The Denton Formation (Lower Cretaceous) was measured at seven localities in Tarrant, Denton, and Cooke Counties. Lithologic samples and fossil collections were taken from the oyster biostrome at the top of the formation.

The fauna collected from the biostrome includes nineteen genera and 24 species of Foraminifera, one species of coral, nineteen genera of bryozoans, eight genera and fourteen species of pelecypods, one species of gastropod, nine genera and seventeen species of ostracods, one species of echinoid, and three species of holothurian sclerites.

Based on living representatives of families, the biostrome is inferred to have been formed in waters of normal salinity except in the most northern localities, and at very shallow depths throughout the entire area although slightly deeper at the southern localities. Turbidity was somewhat less than during deposition of other parts of the Denton Formation and semi-tropical to tropical temperatures are indicated. Reduction in turbidity apparently allowed the biostrome to begin growth and increase in turbidity probably ended growth.

One of the most important aspects of the biostrome is the change in fauna from a dominance of *Gryphaea washitaensis* Hill in the southern localities to *Ostrea* (*Arctostrea*) *carinata* Lamarck and then *Ostrea* (*Lopha*) *quadriplicata* Shumard in the most northern localities.

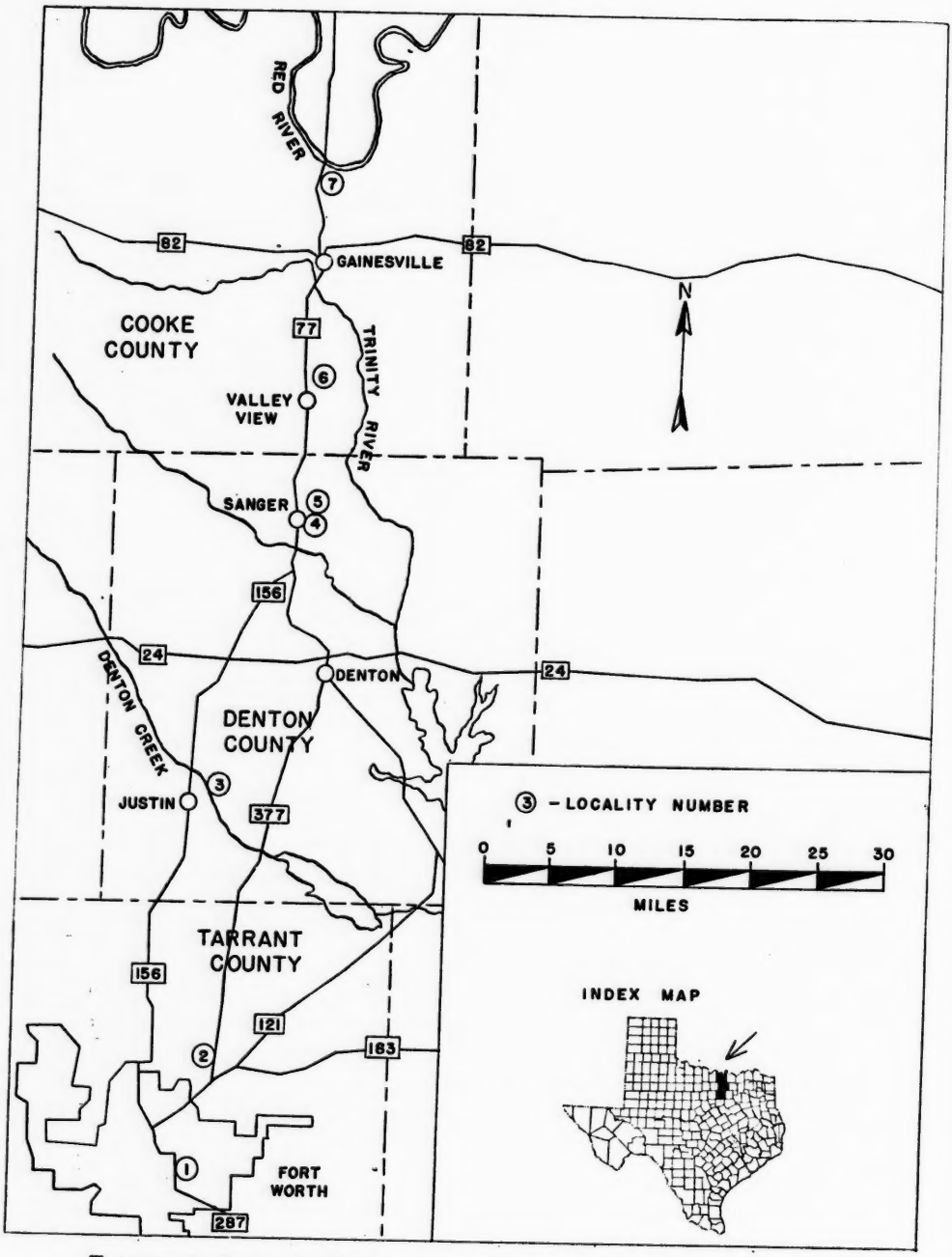
INTRODUCTION AND PREVIOUS WORK

THIS paper presents results from a study of the fauna and sediments found in the biostrome at the top of the Denton Formation. The formation is part of the Washita group of the Comanche Series (Adkins, 1932) and is equivalent to part of the Upper Albian Stage of Europe. Sections of the Denton were measured and sampled from Fort Worth northward to the Red River (Text-fig. 1).

Outcrops of the Denton Formation extend in a north-south direction through northern Texas. At the Red River the formation is 63 feet thick (Slocki, 1956), whereas at Austin the Denton is represented by a *Gryphaea washitaensis* Hill shell bed only two feet thick (Cuyler, 1929).

South of Austin, the Denton Formation is not recognized and is considered to be equivalent to part of the Georgetown Limestone. In Oklahoma, the Denton is equivalent to a clay member within the Bokchito Formation (Bullard, 1926). The outcrop essentially follows the Red River, but the eastward limit is not known. Hill in 1888, stated that the biostrome of the formation is found from Oklahoma to the Arkansas line. He also recognized the "horizon of the *Gryphaea pitcheri*, with *Ostrea carinata*" which is at the top of the Denton Formation, but he did not give the eastward extent of the horizon.

In 1889, R. T. Hill defined a group of beds, lying between the now recognized Fort Worth and Woodbine formations, as the Denison Beds. He later (1894) divided the Denison Beds into four members, the lowest of which he called the Marietta Beds; however, Taff (1892) two years previously described a section on Denton Creek east of Justin and called this section the Denton marl. Hill (1900) again divided the Denison Beds into three subgroups. The lowest subgroup, called the Denton Subgroup, had the same limits at the same locality as Taff's Denton Marl. Adkins (1932) recognized Taff's terminology and placed the Denton formation within the Washita Group. Stephenson *et al.* (1942) essentially followed the usage of previous workers, and in addition considered the Denton as one of the middle members of the Georgetown Limestone in Central Texas. These writers also considered the Denton as the basal member



TEXT-FIG. *1*—Denton localities in Tarrant, Denton, and Cooke Counties, Texas.

of the Denison Formation of the Washita Group in North Texas. Perkins & Albritton (1955) considered the Denton as having formational status within the Washita Group.

The term "bank" is used in this paper for a skeletal limestone deposit formed by organisms which do not have the ecologic potential to erect a rigid wave-resistant structure.

All samples and fossils are housed in the Paleontological Museum at Southern Methodist University.

The author wishes to acknowledge the help and guidance given by D. L. Clark in preparation of this paper, to Dan Feray for information on recent marine ecology, and to Arthur Richards for making equipment and facilities of the Department of Geology, Southern Methodist University, available.

THE DENTON BIOSTROME

Table 1 shows the stratigraphic and geographic occurrence of the fossils found in the Denton Biostrome.

A rather striking feature of the biostrome is the abundance in number and variety of Bryozoa. These have been tentatively identified to generic level but, since little previous work has been done on Texas Cretaceous bryozoans, the identifications are subject to verification.

Several types of holothurian sclerites were found, but the forms are evidently undescribed species. Several new ostracods and small pelecypods were also collected.

PALEOECOLOGIC IMPLICATIONS OF THE DENTON FORMATION FOSSILS

Temperature, salinity, depth, oxygenation, light penetration, and bottom conditions are the main ecologic limiting factors that should be determined, if possible, in a marine paleoecologic study. Inferences about these limiting factors may be drawn from the fossil assemblages and the sediments that enclose these assemblages. The morphology of a fossil may be indicative of its life habits. Any inferences drawn from the form or structure of the organism should be closely analyzed, for some groups of organisms show poor correlation between habit and morphology.

A serious difficulty in paleoecologic study is the problem of mixing of faunas before burial. Evidence such as burial in life position, well preserved rather delicate fossils, or parts of organisms which may easily fall apart after death but are found together, infers that the fossils lived at or near the point of burial. The foregoing criteria are not infallible. For example a shell may be washed back and forth breaking and abraiding it but never leaving the site where it had lived.

The texture and composition of the sediments should be taken into consideration in determining the paleoecology. The turbidity and bottom conditions which affect organic assemblages are inferred by a study of the rocks in which the assemblages are found.

Because none of the species found in the biostrome are living today, inferences as to the paleoecology of each species are based upon the ecology of living species in the same genus or even upon other genera in the same family. To base the paleoecology on another organism in the same family is rather tenuous and may be misleading, but the information concerning family ecology is better than no basis at all.

Foraminifera.—The only representatives of the phylum Protozoa found in the Denton belong to the subclass Foraminifera. Glaessner's classification (1947) is used. Any reference to the classification by Cushman (1948) is indicated.

Lozo (1943b) observed that Foraminifera are generally rare in oyster banks and although the Foraminifera fauna from the Denton Biostrome is not as large as those in other parts of the Lower Cretaceous, some 24 species were identified.

Loeblich & Tappan (1950) found that a typical brackish-water assemblage is dominated by large arenaceous forms with only a few small calcareous ones. Cold water at shallow depths may be indicated by an arenaceous assemblage of Foraminifera (Glaessner, 1947). Stainforth (1952), on the other hand, believes that an assemblage of Foraminifera dominated by large robust arenaceous forms is the result of turbid conditions rather than conditions of temperature or salinity. In the Santa Cruz Basin of California arenaceous tests are limited to depths of less than 800 meters (Resig, 1958).

TABLE 1—FOSSIL LIST OF THE DENTON BIOSTROME

	BIOFACIES	A							B							C							D						
	LOCALITY	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
FORAMINIFERA	*Anomalina petita*	×																											
	Citharina kochii var. *kochii*																			×		×							
	Citharina kochii var. *striolata*			×														×											
	Dentalina communis	×															×												
	Discorbis minima		×	×	×																								
	Epistomina charlottae																					×							
	Epistomina lacunosa															×				×									
	Gaudryina (Gaudryina) cushmani		×	×		×												×	×	×		×		×					
	Globigerina washitaensis			×														×						×					
	Haplostiche texana				×		×	×												×		×							
	Lenticulina cyprina			×	×	×	×									×	×		×	×									
	Lenticulina gaultina		×	×		×		×									×	×	×	×									
	Nodosaria barkeri	×																											
	Patellina subcretacea						×																						
	Placopsilina minima			×				×																					
	Reophax deckeri							×																					
	Siphotextularia washitaensis																					×							
	Spiroplectammina ammovitrea																							×					
	Spiroplectammina goodlandana																	×											
	Textularia losangica																			×									
	Textularia rioensis	×			×	×																							
	Tristix gigantea	×																											
	Tri tix quadrata																			×									
	Valvulineria asterigerinoides			×																									
CORAL	*Micrabacia?* sp.				×			×																					
BRYOZOAN	*Aplousina* sp.		×		×	×													×	×			×						
	Ceriopora sp.				×	×													×		×	×							
	Chartecylis sp.																			×									
	Conopeum sp.																							×					
	Discofascigera sp.			×																									
	Elea? sp.																			×									
	Filisparsa sp.																	×		×									
	Fungella sp.				×	×																							
	Homeosolen sp.				×	×																							
	Laterocavea sp.			×	×								×						×	×									
	Meliceritites sp.																			×									
	Membraniporidra sp.			×																				×	×				
	Plagioecia sp.															×								×	×				
	Reptomullicava sp.					×										×				×									

TABLE 1—*continued*

	BIOFACIES	A							B							C							D						
	Locality	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
	Seminodicrescis sp.																		×										
	Stamenocella sp.					×																							
	Stomatopora sp.					×													×										
	Thyracella sp.																			×									
	Vinella sp.				×																								
MOLLUSK	*Gervilliopsis invaginata*														×							×							×
MOLLUSK	*Gryphaea washitaensis*	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		
MOLLUSK	*Lima (Mantellum) wacoensis*														×														
MOLLUSK	*Lima (Mantellum) wacoensis* var. *quadrangularis*																							×					
MOLLUSK	*Ostrea (Arctostrea) carinata*			×	×	×	×					×	×	×	×		×	×	×	×	×	×			×		×		
MOLLUSK	*Ostrea (Lopha) quadriplicata*			×	×	×		×						×	×				×	×	×	×			×		×	×	×
MOLLUSK	*Ostrea (Lopha) subovata*														×												×		
MOLLUSK	*Pecten (Neithea) bellulus*													×															
MOLLUSK	*Pecten (Neithea) georgetownensis*				×																						×		
MOLLUSK	*Pecten (Neithea) subalpinus*																								×	×			
MOLLUSK	*Pecten (Neithea) texanus*			×	×	×	×		×		×	×	×		×	×	×		×	×	×	×	×			×	×	×	×
MOLLUSK	*Plicatula dentonensis*			×	×	×	×	×						×		×	×		×	×					×	×		×	×
MOLLUSK	*Protocardia texana*							×																					
MOLLUSK	*Trigonia clavigera*							×						×															×
MOLLUSK	*Turritella delriensis*																						×						
OSTRACOD	*Brachycythere? subconcentrica*																					×							
OSTRACOD	*Cythere concentrica*							×																					
OSTRACOD	*Cythereis dentonensis*	×	×	×	×	×	×	×									×	×	×	×		×		×					
OSTRACOD	*Cythereis hawleyi*					×													×	×									
OSTRACOD	*Cythereis nuda*		×																	×									
OSTRACOD	*Cythereis ornatissima*				×																								
OSTRACOD	*Cythereis paupera*															×													
OSTRACOD	*Cythereis pustulosissima*																		×										
OSTRACOD	*Cythereis worthensis*				×			×										×											
OSTRACOD	*Cytherella comanchensis*	×	×	×	×	×	×	×									×	×	×	×				×					
OSTRACOD	*Cytherelloidea reticulata*																							×					
OSTRACOD	*Cytherelloidea williamsoniana*														×														
OSTRACOD	*Cytherelloides williamsoniana* var. *stricta*																×	×											
OSTRACOD	*Cytheropteron rugosalatum Paracyprideis graysonensis*	×				×		×														×							
OSTRACOD	*Paracypris alta*		×		×	×		×																×					
OSTRACOD	*Pontocyprella alexanderi*		×														×	×			×			×					
ECHINODERM	*Cidaris (Stereocidaris) hemigranosus*			×	×	×						×		×	×		×	×	×		×	×			×	×	×		
ECHINODERM	Holothuroidea							×													×								

1. Superfamily Lituolidea—An arenaceous assemblage of lituolid Foraminifera indicates shallower depth than a diversified assemblage of calcareous forms (Albritton *et al.*, 1954).
   a. Family Reophacidae—This family, when part of a large, robust, arenaceous assemblage, indicates turbid conditions (Stainforth, 1952).
      (1) *Reophax*—One species (Phleger, 1956) off the Central Texas Coast was discovered at depths of between 20 and 84 meters. Two other species were found off the Texas Coast in water between 33 and 196 meters deep (Phleger & Parker, 1951).
   b. Family Textulariidae—This family is located in relatively shallow water 10 to 120 meters deep (Lozo, 1944). Norton (*in* Vaughn, 1940) found this family to be abundant between the same limits. Stainforth (1952) considers this family's arenaceous forms as indicators of turbid conditions.
      (1) *Textularia*—Two species of this genus were established to live between 20 and 72 meters, off the coast of Texas (Phleger & Parker, 1951). Lozo (1943a) states that the genus is indicative of a warm, shallow-water environment, but Natland (1933) found the genus to be abundant between 90 and 300 meters in depth and 9° to 13° C. *Textularia* is commonly discovered in brackish water (Moore *et al.*, 1952). Phleger (1956) found another species living in a zone between 23 and 85 meters, while Lowman (1949) in his classic study placed the genus between sea level and a depth of 220 meters.
      (2) *Spiroplectammina*—The *Spiroplectammina-Flabellammina* assemblage is found only in gray shale and marl in the Fort Worth area (Lozo, 1944).
   c. Family Verneulinidae—Stainforth (1952) listed this family as an indicator of turbid conditions if large, robust, arenaceous forms were dominant in the foraminifer assemblage.
      Gaudryina—Natland (1933) found this genus to be abundant at one locality off the California Coast from 90 to three hundred meters deep and 9° to 13°C. Phleger (1956) discovered two species off the Texas Coast. One species was restricted to a depth of 62 to 90 meters, and the other was restricted to a depth between 9 and 41 meters. Both species represented only a small percentage of the total population.
2. Superfamily Lagenidea
   a. Family Lagenidae (Cushman)—Norton (*in* Vaughan, 1940) found this group to be abundant in the zone between 10 and 120 meters.
      (1) *Dentalina*—Lozo (1943a) said that this genus indicates a warm, shallow-water environment. *Dentalina* is found at depths between 40 and 175 meters off the Texas Coast (Phleger & Parker, 1951).
      (2) *Lenticulina*—One species living off the Texas Coast is found between 61 and 105 meters and is rare (Phleger, 1956). Another species was discovered between 67 and 132 meters (Phleger & Parker, 1951).
      (3) *Nodosaria*—Lozo (1943a) stated that this genus indicates a warm, shallow-water facies.
3. Superfamily Rotaliidea
   a. Family Spirillinidae
      Patellina—One species inhabits all oceans, and it is restricted to the warm, shallow waters of the littoral zone. The optimum reproduction temperature is 21°C., and the minimum is about 18°C. (Myers, 1935)
   b. Family Discorbidae
      Discorbis—The genus according to Jones (1956) is adapted to brackish water conditions. On the West Coast, Natland (1933) discovered this genus to be abundant from 90 to 300 meters with a water temperature of 9° to 13°C. Along the Texas Coast one species was found from 22 to 49 meters and always deeper than 20 meters (Phleger, 1956). Lowman (1949) established that the genus is present between 20 and 220 meters, while Phleger & Parker (1951) identified three species between 22 and 98 meters off the Texas Coast.
   c. Family Rotaliidae (Cushman)—*Patellina* and *Discorbis* are included in this family. Lowman (1949) found that this family dominates the foraminiferal assemblage midway between the coastline and the continental slope.
   d. Family Anomalinidae—In Cushman's classification *Anomalina* falls within this family, Glaessner (1947) states that the Anomalinidae, like the Rotaliidae, are present at nearly all depths.
   e. Family Globigerinidae
      Globigerina—This genus is planktonic (Moore *et al.*, 1952). The genus becomes a significant part of the foraminiferal fauna from the Mississippi Delta outward (Lowman, 1949).

Coelenterata.—Only one identifiable coral was found in the oyster bank. The following classification comes from Moore *et al.* (1952).

Class Anthozoa

Subclass Zoantharia—This group is confined to marine waters and is most abundant in warm, shallow seas. The solitary forms are found to a depth of 5,870 meters (Moore *et al.*, 1952).

Order Scleractinia—All the early forms seem to have lived in shallow tropical or subtropical waters (Wells, 1957).

Bryozoa.—Nineteen genera of Bryozoa were found in the oyster bank of the Denton Formation. These genera were identified and classified according to Bassler (1953).

"It is generally stated that bryozoans are uncommon in the Jurassic and Cretaceous of North America" (Duncan, 1957). Duncan later adds that "sedimentary facies" were apparently unfavorable, but she suspects the phylum has been overlooked or ignored. If Bryozoa are actually uncommon, then the oyster bank of the Denton Formation is an exception, for they are found in great abundance and variety, particularly in the northern localities.

Jones (1956) says that bryozoans are essentially neritic in habitat and are found in clear waters of both cold and warm seas. Moore *et al.* (1952) agree, but they state that bryozoans were most abundant in temperate and tropical areas. Osburn (1957) points out that the great majority of Bryozoa live in the zone from low tide to 200 to 400 meters but may live much deeper than this. Bryozoa are not found in estuarine waters where the salinity is very low. Below 20 parts per thousand the bryozoan fauna is greatly reduced in number of species, but the species present may be very abundant.

1. Order Ctenostomata—Prior to the Mesozoic the Ctenostomata were very abundant, but beginning in the Mesozoic this order became very rare (Bassler, 1953), *Vinella* belongs in this order.
2. Order Cyclostomata—This order was dominant in the Mesozoic until Late Cretaceous when the Cheilostomata became dominant (Bassler, 1953).
   a. Family Diastoporidae—Maturo (1957) found one species belonging to this family living at a depth of about 26 meters. This species' range is from Beaufort, North Carolina, through the Gulf of Mexico. This family includes *Stomatopora.*
   b. Family Oncousoenciidae—One species of the family occurs offshore near Beaufort (Maturo, 1957).
3. Order Cheilostomata—This order has evolved hydrostatic apparatus that permits them to adapt to greater depths than the other groups (Duncan, 1957).
   a. Family Membraniporidae
      Conopeum—This is a membraniform type cheilostomate. According to Stach (1936) this type of cheilostomate is limited to the littoral and sublittoral areas. It is found in deeper water but is rare. This genus is found off the coasts of France and England (Canu & Bassler, 1920) and one species ranges from Beaufort to Brazil. This species is found in these warm waters at a depth of about 13 meters (Maturo, 1957).
   b. Family Hincksinidae
      Aplousina—Like *Conopeum*, *Aplousina* is membraniform and thus is littoral and sublittoral (Stach, 1936). One species is found off the coast of Georgia, common in the Florida straits, and the Gulf of Mexico. It is found from 6 to 112 meters (Maturo, 1957).
   c. Family Calloporidae
      (1) *Membraniporidra*—This genus is also a membraniform type cheilostomate; thus it is limited mainly to the littoral and sublittoral zone (Stach, 1936).
      (2) *Stamenocella*—This genus has a escharifform type of zooaria, and thus was adapted for life in the sublittoral zone at depths of at least 20 meters (Stach, 1936).
   d. Family Onychocellidae
      Thyracella—This genus has a vinculariform type zooaria, which indicates growth in quiet water where wave action is absent and currents weak (Stach 1936).

Pelecypoda.—The oysters are especially abundant at the top of the Denton Formation. Fourteen species are found in the bank. Classification follows that of Moore *et al.* (1952).

Hopkins (1957) pointed out that a prerequisite for a rich pelecypod fauna is an abundant plankton supply, and that large plankton populations thrive best in agitated waters.

1. Suborder Trigoniacea
   Trigonia—Living species of *Trigonia* are found only in Australia. They are particularly abundant in the Sidney Harbor (Tryon, 1884).
2. Suborder Spondylacea
   Plicatula—The genus is found off the coasts of India, West Indies, Philippines, Australia, and West America (Tryon, 1884). One species (*gibbosa*) that is morphologically similar to *P. dentonensis* lives from intertidal to offshore (Abbot, 1954). The modern *Anomia*, like *Plicatula dentonensis* Cragin has many different shell forms. If in calm water *Anomia* will have a smooth shell, while if grown in rough water it will have a corrugated shell (Winton, 1925). *Plicatula dentonensis* Cragin, however, also has a spinose shell under certain conditions.
3. Suborder Ostreacea
   a. *Gryphaea*—Jourdy (*in* Bergquist & Cobban, 1957) concluded that *Gryphaea* represented greater salinity and depth than did *Ostrea.* Vokes (1948) believes that small oyster spats are killed before reaching maturity because of rapid silting.

b. *Ostrea*—The genus seems to prefer a sandy bottom, near shore, and in shallow water (Vokes, 1945). Species of *Ostrea* s.s. live in more saline, less turbid, and somewhat deeper water than *Crassostrea virginica*. *Ostrea* lives on shallow banks in the sea and does not form massive reefs.

4. Suborder Limacea—The group is found chiefly in tropical and temperate seas on sandy or muddy bottoms. The group has a wide depth toleration (Tryon, 1884).
   Lima—The modern species are found off Norway, Britain, West Indies, Canaries, India, and Australia (Tryon, 1884).
   Lima (*Mantellum*)—One species is found from Monterey, California, to Mexico.

Gastropoda.—The classification of the gastropods follows that of Shimer & Shrock (1944). Many types of gastropods were found in this study, but they were commonly internal molds and thus difficult to identify.

Superorder Prosobranchia
Order Mesogastropoda
Superfamily Ceritheacea—A dominance of this superfamily indicates a brackish water environment (Vokes, 1948).
Turritella—Tryon (1883) stated that this genus had worldwide distribution, ranging from the littoral zone to 200 meters. The four American species live in semi-tropical to tropical waters. Most are shallow-water forms, although one species is found as deep as 200 meters (Abbott, 1954).

Ostracoda.—Seventeen species of Ostracoda are listed.

Although foraminifers are commonly scarce in an oyster bank, ostracods may be more abundant than in other beds. Lozo (1943b) believes this to be the result of physico-chemical conditions which are favorable to oysters and ostracods and unfavorable for foraminifers. In this study it was found that the ostracods were commonly more abundant than the foraminifers, but the reverse was often true at some localities and often both groups were rare.

1. Family Cytherellidae
   a. *Cytherelloidea*—Lozo (1943a) interpreted their presence as indicative of a warm, shallow-water environment.
   b. *Paracypris*—This genus occurs in a warm, shallow-water environment (Lozo, 1943a). Sohn (1957) states that it is strictly a marine form.
2. Family Cytheridae
   a. *Cythere*—This genus is tolerant of brackish to marine water (Sohn, 1957).
   b. *Cythereis*—Lozo (1943a) believed this genus indicated a warm, shallow-water environment. Modern forms are very tolerant of reduced salinity, but their ancestors apparently were not as tolerant (Sohn, 1957).
   c. *Cytheropteron*—This genus is indicative of warm, shallow-water environment (Lozo, 1943a). It is tolerant of brackish to marine water (Sohn, 1957). Stadnichenko (1927) thought the presence of this group indicated more or less shallow seas in the temperate zone.

Echinoidea.—Many echinoid spines and plates were found, but only the spines and plates of one regular echinoid were distinctive enough for identification. Pieces of several irregular echinoids were found, but they were unidentifiable. The classification is after Moore *et al.* (1952).

Lozo (1943b) thought the presence of echinoid remains indicated normal salinity. They live from the intertidal zone to abyssal depths (Moore *et al.*, 1952).

Subclass Regularia—In agitated water this group is restricted to hard bottoms or bioherms (Moore *et al.*, 1952).
Cidaris—This genus would be stifled by a sand or ooze bottom (Hawkins, 1943).

Holothuroidea.—Frizzell & Exline (1955) have pointed out that holothurians are abundant in shallow, tropical waters, but they are much rarer in shallow polar seas. The group is almost exclusively sessile or vagrant benthos, and almost all modern forms live in normal marine water.

Family Calclaminidae.—This family's mode of life is "burrowing, crawling on or partly submerged in a sea-floor, or clinging to rocks of seaweed" (Frizzell & Exline, 1955, p. 44).

PALEOECOLOGY OF THE DENTON OYSTER BIOSTROME

The beds of the Denton Biostrome with a clay or marl matrix were easily disaggregated and the fauna studied in detail. This was not possible in the case of limestones, so a more varied fauna may appear to be present in the shales and marls than in the limestones. Actually, faunal assemblages were well developed in the limestones, and as many identifications as possible were made from exposures on weathered surfaces.

The term biofacies is used in this paper according to Glaessner's definition. A biofacies is defined as "assemblages formed at the same time under different conditions"

(1947, p. 183). The Denton Biostrome is divided into four biofacies and each biofacies is represented at all the localities (Text-fig. 2).

Hill (1900) and Stanton (1928) considered the Washita sea bottom to dip toward the south and southeast. Scott (1940) thought that the beds marked by large quantities of *Ostrea* and *Gryphaea* represented depths of less than 20 fathoms. By inference the consensus is that the Denton Biostrome occurs within the epineritic zone with the sea bottom gently sloping to the south and southeast.

The three dominant pelecypods of the biostrome are *Gryphaea washitaensis* Hill, *Ostrea* (*Arctostrea*) *carinata* Lamarck, and *Ostrea* (*Lopha*) *quadriplicata* Shumard. The presence of each of these three species varies both geographically and stratigraphically. The ecologic factors that apparently controlled their presence were depth, salinity, and turbidity.

Gryphaea washitaensis is present in almost all the beds regardless of geographic position or lithology. This species is not present in certain beds containing arenaceous foraminifer assemblages dominated by arenaceous forms, inferring deposition under conditions of slightly reduced salinity. From its occurrence at the most southern localities and abundance in shale beds, *Gryphaea washitaensis* was probably sensitive to reduced salinity as indicated by the above mentioned arenaceous foraminifer assemblages.

Ostrea (*Arctostrea*) *carinata* is almost exclusively restricted to limestones and marls and occurs mostly in the middle and northern localities, which because of the dominance of arenaceous foraminifers are interpreted to have had slightly reduced salinity. *Ostrea* (*Arctostrea*) *carinata*, because of its rarity in shale beds, is inferred to have been sensitive to turbidity. Because its first occurrence in a biofacies is farther north than the abundant *Gryphaea washitaensis*, *Ostrea* (*Arctostrea*) *carinata* was probably restricted to depths shallower than those in which *Gryphaea washitaensis* could survive. *Ostrea* (*Arctostrea*) *carinata* probably lived in both normal marine water inhabited by *Gryphaea washitaensis* and also in the above mentioned areas of slightly reduced salinity.

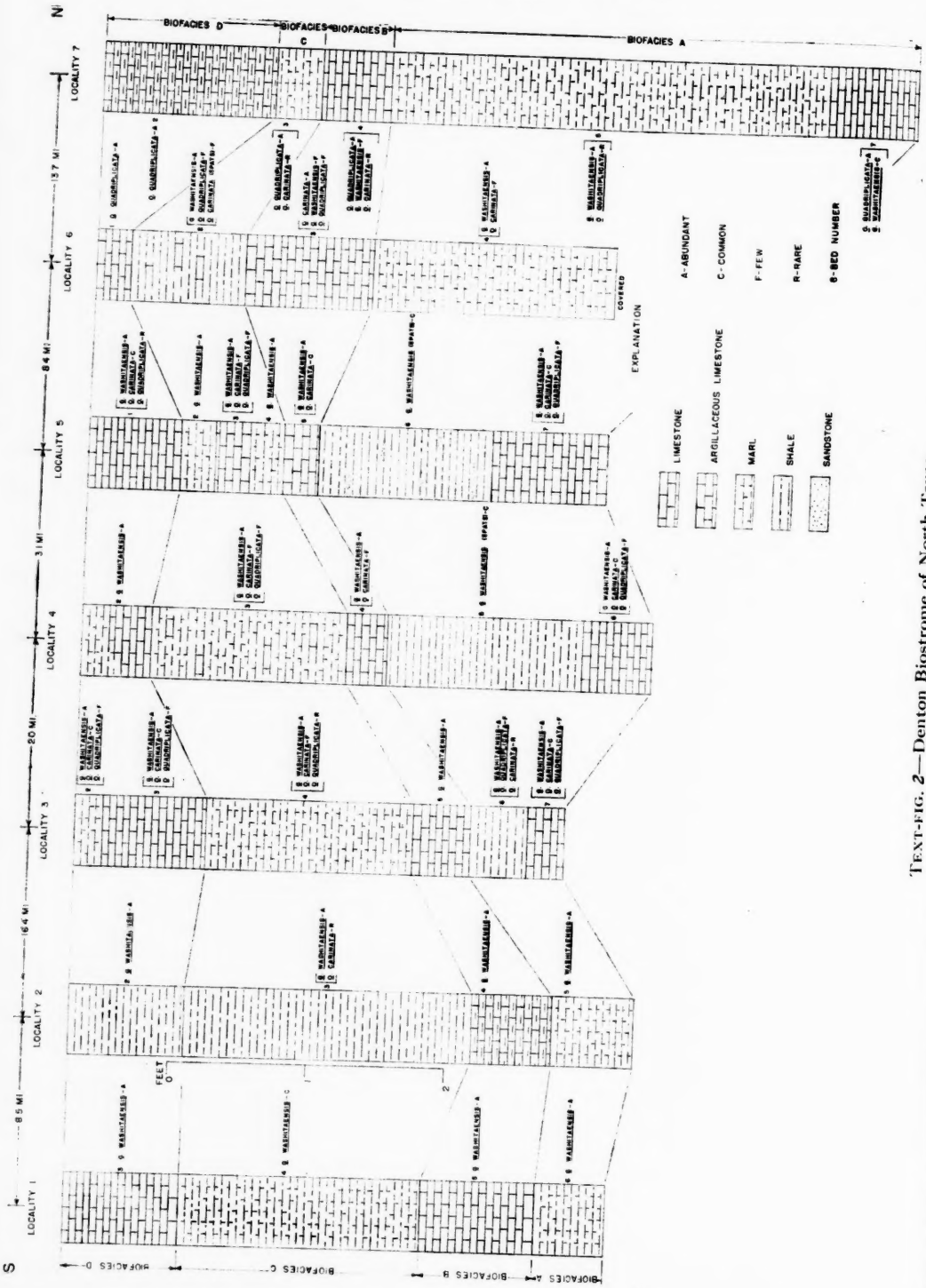
Ostrea (*Lopha*) *quadriplicata* is restricted to beds in the middle and northern localities (first occurrence of the species in a biofacies is often farther northward than the first occurrence of *Ostrea* (*Arctostrea*) *carinata*), and this species is found in shales as well as limestones. *Ostrea* (*Lopha*) *quadriplicata* is also found in beds inferred to have been deposited in water of slightly reduced salinity. This inference is based upon the presence of a foraminiferal assemblage dominated by arenaceous forms. As a result of its near-shore distribution in the biofacies, it is inferred that *Ostrea* (*Lopha*) *quadriplicata* was not as tolerant of rather deep water as either *Ostrea* (*Arctostrea*) *carinata* or *Gryphaea washitaensis*. Possibly *Ostrea* (*Lopha*) *quadriplicata* was even more tolerant of reduced salinity than *Ostrea* (*Arctostera*) *carinata* for certain northern locality limestones beds were probably deposited in an environment of reduced salinity, *Ostrea* (*Lopha*) *quadriplicata* is the only oyster present.

Biofacies A.—This biofacies (Text-fig. 2) includes that portion of the Denton Formation indicated on Text-figure 3.

There are three significant paleoecologic features of this biofacies. First, there is a limestone at the base of the biofacies at all but the two most southern localities (base covered at locality 6). The second feature consists of a change from dominance of *Gryphaea washitaensis* Hill in the lower limestone bed at the middle localities to dominance of *Ostrea* (*Lopha*) *quadriplicata* Shumard at the most northern locality. The third important feature is the inferred rapid argillaceous sedimentation above the limestone as shown at localities 4 and 5.

The limestone bed at the base of the biofacies at the middle and northern localities probably has its equivalent in the lower part of the marls at the southern two localities (localities 1 and 2). Possibly, while clearer water conditions prevailed to the north, some argillaceous material was being transported to the southern localities from the east or west.

The lower limestone bed at the middle localities infers slow deposition in clear water. The relatively abundant fish remains and bryozoans strengthen the contention for slow deposition. Both the gradual, but



TEXT-FIG. 2—Denton Biostrome of North Texas.

steady, change in dominance from *Gryphaea washitaensis* Hill at locality 3 to *Ostrea* (*Lopha*) *quadriplicata* Shumard at locality 7 and the bryozoan and microfauna assemblages indicate a decrease in depth northward.

During the deposition of the upper part of the biofacies the water was apparently more turbid than during the deposition of the earlier limestone bed. This increase of argillaceous deposition was particularly great at localities 4 and 5 where the *Gryphaea washitaensis* Hill were killed, presumably by siltation, while still in the spat stage (juveniles). The high turbidity at these two localities is reflected in the foraminifer fauna, which is dominated by arenaceous forms. The relatively higher rate of sedimentation at these middle localities than at those localities to the north and south may have been the result of argillaceous material coming from the east or west, rather than directly from the landmass to the north.

Within the argillaceous part of Biofacies A the fauna indicates more shallow waters in a northward direction, but sedimentation was probably rapid enough at even the most northern (shallow) localities to prevent the species of *Ostrea* from becoming the dominant pelecypod.

The fauna of Biofacies A infers semitropical to tropical temperatures. The depth of water from locality 1 through locality 7 was probably shallow neritic, and the salinity is inferred to have been normal marine.

Biofacies B.—The beds included within this biofacies are indicated on Text-figure 3. This biofacies has two important characteristics. First, it is represented by a limestone at every locality, and this limestone is surprisingly uniform in thickness throughout, and second, since there was little or no argillaceous material being deposited to disturb the succession of oysters into shallow water, there was an orderly change in dominance from *Gryphaea washitaensis* Hill at the southern and middle localities through *Ostrea* (*Arctostrea*) *carinata* Lamarck (loc. 6) to *Ostrea* (*Lopha*) *quadriplicata* Shumard (loc. 7).

The constant thickness of this biofacies is illustrated by comparing locality 3, bed 5 and locality 5, bed 5. Although these two localities are more than 23 miles apart the difference in thickness is only two inches. This uniformity of limestone lithology and thickness infers rather quiet water over a wide area.

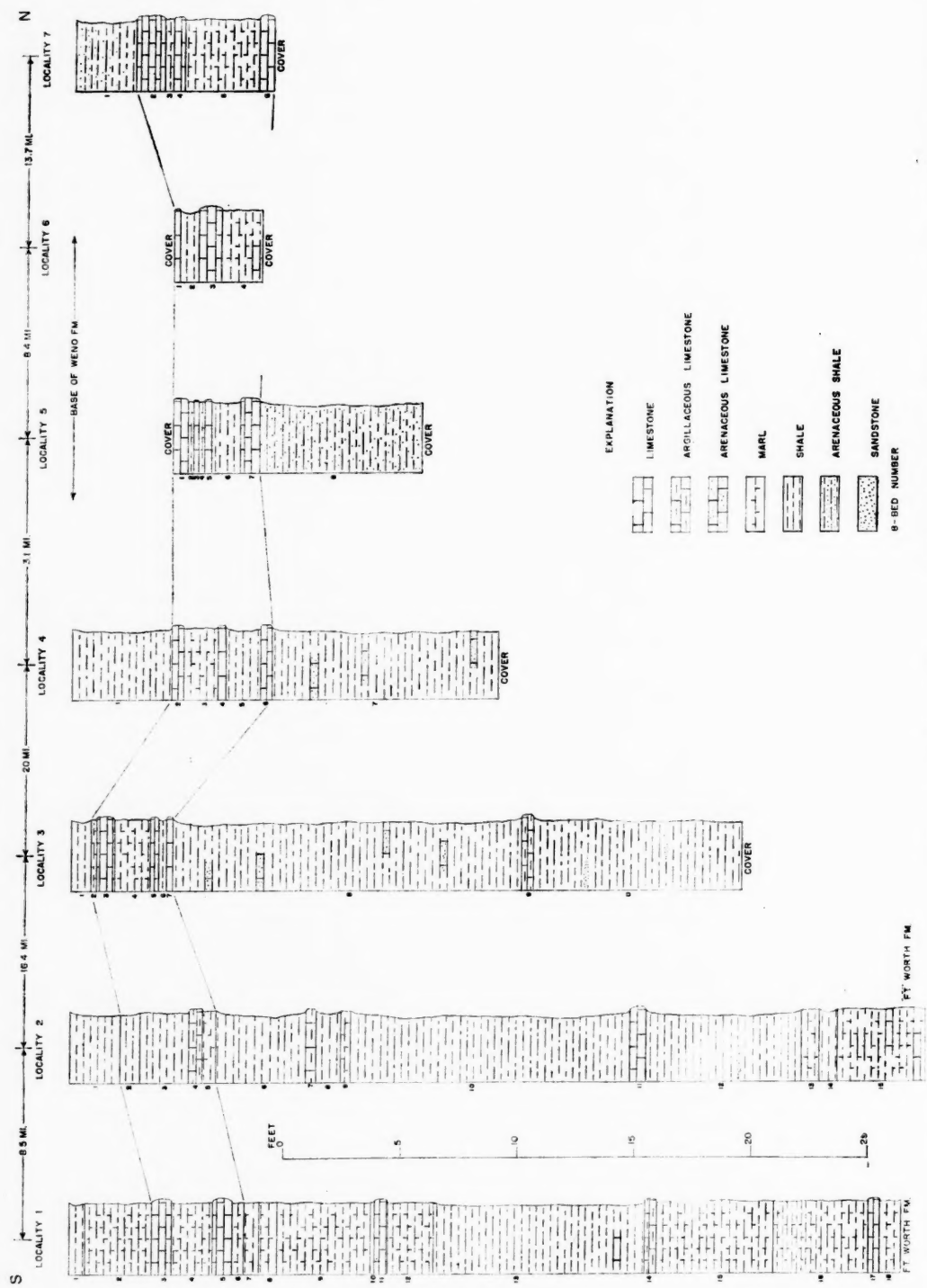
At the two southernmost localities the water was deep enough that only *Gryphaea washitaensis* Hill was present. Probably at the position of locality 3 the water was shallow enough that a few *Ostrea* (*Arctostrea*) *carinata* Lamarck could survive. Continuing northward to localities 4 and 5 the *Gryphaea washitaensis* Hill were still dominant, but the water was probably shallow enough so that *Ostrea* (*Arctostrea*) *carinata* Lamarck are common. At locality 6 *Ostrea* (*Arctostrea*) *carinata* Lamarck were the dominant oysters, and only a few *Gryphaea washitaensis* Hill and *Ostrea* (*Lopha*) *quadriplicata* Shumard are present. This association of oysters infers shallower water than the more southern localities. *Ostrea* (*Lopha*) *quadriplicata* Shumard is the dominant oyster at the most northern locality (locality 7) with subordinant *Gryphaea washitaensis* Hill and *Ostrea* (*Arctostrea*) *carinata* Lamarck. This oyster assemblage infers that locality 7 is the shallowest locality of the biofacies.

The fauna of Biofacies B infers normal marine salinity and warm shallow water conditions of deposition.

Biofacies C.—This biofacies is indicated on Text-figure 3. There are three rather significant features in this biofacies. One is the somewhat steady change of dominant species of oysters from the southern to the northern localities. The second feature is the varied populations of bryozoans, foraminifers, and ostracods. The third feature is the relatively large percentage of sand size particles as compared with the total insoluble residue at the northern localities.

At the most southern localities (localities 1 and 2) of Biofacies C the only oyster present is *Gryphaea washitaensis* Hill. The middle localities (localities 3, 4, 5, and 6) also exhibit *Gryphaea washitaensis* Hill as the dominant fossil, but a few *Ostrea* (*Arctostrea*) *carinata* Lamarck and *Ostrea* (*Lopha*) *quadriplicata* Shumard are also present. This oyster association and bryozoan assemblages at the middle localities infer shal-

TEXT-FIG. 2—Denton Biostrome of North Texas.



TEXT-FIG. 3—Denton Formation in North Texas.

lower, less turbid conditions than at the two southern localities. The dominance of *Ostrea* (*Lopha*) *quadriplicata* Shumard and absence of *Gryphaea washitaensis* Hill at locality 7 along with the foraminifer assemblage infers very shallow water accompanied by at least a periodic slight reduction in salinity.

The varied bryozoan, foraminifer, and ostracod populations of this biofacies may not be due to larger populations than present in other biofacies, but merely because the shales and marls were easily broken down and studied.

The relatively large percentage of sand size particles as compared with the total insoluble residue at locality 7, and to a lesser extent at locality 6, indicates deposition of sand size particles relatively near-shore with a smaller percentage being deposited farther offshore. Although locality 7, bed 3 does contain a greater percentage of sand size particles of the total residue than any other bed studied, the sand size particles represent only 3.71 percent of the total.

Biofacies C was probably deposited in slightly turbid water, which was shallower to the north.

Biofacies D.—The beds composing Biofacies D are indicated in Text-figure 3. Biofacies D has two rather important paleoecologic characteristics. One is the tendency at several localities for the biofacies to become more argillaceous upward. The other characteristic is the presence of only one oyster species, *Ostrea* (*Lopha*) *quadriplicata* Shumard, at the northern localities.

The middle localities (localities 3 and 4) of the biofacies indicate that the rate of deposition of argillaceous material increased during the deposition of the upper part of the biofacies. The effects of this increase in argillaceous sedimentation are inferred at locality 3, beds 2 and 3. In the lower part of the biofacies at this locality, silt sensitive *Ostrea* (*Arctostrea*) *carinata* Lamarck were able to mature in clear water, but as the rate of clastic sedimentation increased only juvenile *Ostrea* (*Arctostrea*) *carinata* Lamarck grew along with other more turbidity-tolerant oysters. This steady increase in the rate of sedimentation finally killed all the oysters and ended the life of the biostrome.

The exclusive presence of *Ostrea* (*Lopha*) *quadriplicata* Shumard as the only oyster species at the northern localities, infers that possibly the salinity was reduced at least temporarily. The fauna of the more southern localities in the biofacies infers normal salinity.

The argillaceous character of the biofacies at locality 2 as opposed to the limestone at the other localities infers that the clay size material came from the landmass to the north.

The faunal associations of Biofacies D, as in the earlier biofacies, infers tropical or semi-tropical temperatures. The depth of water in which this biofacies was deposited was shallower to the north, and all the localities infer deposition in the upper part of the neritic zone.

CONCLUSIONS

Recurrent oyster biostromes are common in the Lower Cretaceous of North Texas. The presence of the biostrome at the top of the Denton Formation was probably controlled by a temporary reduction of turbidity within the range of tolerance of the oysters. When the turbidity increased, the oysters were destroyed and growth of the biostrome ended.

The fauna of the biostrome allows the inference that the entire area of study was within the upper part of the neritic zone. Studies of localities in Oklahoma give information indicating a littoral environment.

The fauna collected from the Denton Biostrome has strong affinities to modern forms found in tropical or semi-tropical waters. Oxygen isotope test of original shell material may be helpful in establishing the water temperature during this part of geologic history.

The fauna composing the biostrome indicates normal marine salinity everywhere except certain beds at localities 6 and 7. Some observers have interpreted this and other oyster banks of the Washita Group as a littoral, brackish-water environment. Because the bank in the Fort Worth area was at least 70 miles offshore it is hard to imagine reduced salinity. In the very shallow parts of the bank (locality 7) heavy rainfall or rapid run-off from northern landmasses may have reduced the salinity at times, at least temporarily.

TEXT-FIG. 3.—Denton Formation in North Texas.

The biostrome is discernible from Oklahoma to Austin, Texas, and shallow-water limestones (Georgetown) are found many miles southward and eastward. This condition would indicate a very wide, flat shelf.

It appears that almost all the argillaceous material from the landmass to the north flocculated before it reached the area of deposition of the Georgetown Limestone.

R. T. Hill (1900) concluded that the Washita shore line ran westward along the Ouachita Mountain System to about the ninety-ninth meridian. Stanton (1928) drew a map of the Washita shoreline based upon Washita equivalent rocks found in New Mexico, Colorado, and Kansas. Stanton's shoreline, as opposed to Hill's, swings northward through the Panhandle. Stanton also has a curious southward inflection of his shoreline just west of the present Washita outcrop. The writer found little or no evidence that the localities around Fort Worth were near-shore. The outcrop of the Denton Biostrome swings eastward in southern Oklahoma, and the known outcrops (Bullard, 1926) exhibit a fauna similar to that at locality 7. The shoreline, inferred from the biostrome, ran north of and approximately parallel to the Red River.

Determinations of the paleoecology of the arenaceous foraminifers in this study seem to bear out Stainforth (1952) in his contention that turbidity as well as reduced salinity may result in a dominantly arenaceous foraminifer assemblage.

The four biofacies discussed in this report have been assumed to be essentially time parallel rather than time transgressing facies. If these biofacies crossed time lines as the result of a transgressing or regressing sea, essentially the same faunal assemblage should be present throughout the biofacies; that is, the same faunal assemblage would move with the environment as the sea transgressed or regressed. The fossil assemblages in the biofacies indicate progressively more shallow water and changes in fauna, rather than one community following its optimum environment as conditions changed.

It would seem that the pelecypods and other slowly evolving conservative faunal groups would be better adapted for paleoecologic interpretation than other rapidly evolving groups more commonly used. Another advantage in using the pelecypods is the large amount of ecologic data available and the relative ease in studying their ecology.

An enigma of the biostrome is the apparent lack of oyster predators. Possibly some of the gastropods and regular echinoids found within the reef preyed upon the oysters, but none of the oyster shells shows any sign of boring other than small surficial cavities probably caused by boring sponges after death. Slocki (1956) reported starfish from the Denton Formation. The writer did not find starfish at any of the localities listed in this report, but the easy disassociation of these invertebrates after death may indicate their absence is more apparent than real.

In preparing this paper an effort was made to determine the paleoecology of single beds with no reference to their lateral equivalents. Often gross errors were made in interpretation and it was found that only through regional relationships can a fairly accurate picture of the paleoecology be made.

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PTYCHOBLASTUS, A NEW MISSISSIPPIAN BLASTOID FROM MISSOURI

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ABSTRACT—A new genus, *Ptychoblastus*, is recorded from the Warsaw limestone formation, at Keyes Summit, St. Louis County, Missouri. The type species, *Ptychoblastus pustulosus* Fay, n. sp., has one hydrospire fold on each side of an ambulacrum and a hydrospire plate and associated pores along the margins of the deltoids. The latter feature is a new structure reported to be present in blastoids.

THE Warsaw limestone near Keyes Summit, St. Louis County, Missouri, is exposed in a series of outcrops along the right-of-way of the St. Louis & San Francisco and Missouri Pacific Railroads. The rocks dip about four degrees northeastward and form part of the type Meramecian Series, with the Salem limestone above and the Keokuk-Burlington formations below. The exact location is the SW¼ NW¼ SW¼ sec. 9, T. 44 N., R. 5 E., near top of the bluff southeast of the Missouri Pacific Railroad, and below the level of the St. Louis & San Francisco Railroad. The stratigraphic section exposed in this cut and just to the northeast is:

Description	*Thickness in feet*
Salem limestone (at top)	
Warsaw limestone:	
Shale, yellowish brown, laminated, plastic, with occasional layers of gray medium-crystalline well indurated fossiliferous limestone, weathering into a yellowish brown soil, forming a slope	10.0+
Limestone, light gray, medium to coarsely crystalline, thin-bedded, crinoidal, fossiliferous, with interbedded yellowish brown shale as above. The lower three feet is shaly and extremely fossiliferous, containing *Ptychoblastus* and many crinoids	5.0
Limestone, light gray, medium-granular, well indurated, fossiliferous, massive, with a two-inch chert layer at top, forming ledge	1.7
Limestone, light gray to yellowish gray, medium to coarsely crystalline, wavy-bedded, medium-bedded, fossiliferous, with occasional shale layers and reddish brown to gray chert nodules	5.75
Limestone, light gray to bluish gray, as above, well indurated, in three massive ledges	1.5
Limestone, light gray to bluish gray, mottled tan, fine to coarsely crystalline, crinoidal, fossiliferous, with many *Archimedes*, thin- to medium-bedded, with small irregular chert nodules, interbedded with bluish gray to dark gray to yellowish brown clay shale	8.5
Keokuk limestone?:	
Limestone, bluish gray, crystalline, fossiliferous, wavy-bedded, thin- to medium-bedded, with many chert bands and a few thin yellowish brown to bluish gray clay shale seams, weathering into a resistant unit	11.0
Burlington limestone:	
Limestone, yellowish brown, medium-crystalline, crinoidal, with 50 percent or more of light brown nodular chert, well cemented, resistant, forming a prominent escarpment with underlying beds, exposed to Missouri Pacific track level	5.0

The blastoids occur in the unit that is 12 to 15 feet below the top of the Warsaw limestone, in yellowish brown clay shale. Nine specimens were collected from this unit, all are compressed to some degree. The description and illustrations are based upon examinations of all nine specimens.

Genus PTYCHOBLASTUS Fay, n. gen.
Type species: *Ptychoblastus pustulosus* Fay, n. sp.

This genus includes spiraculate blastoids with an elliptical-shaped outline, eight separate spiracles exposed, and two additional spiracles on the anal side fused with the anal opening. The anal opening is be-

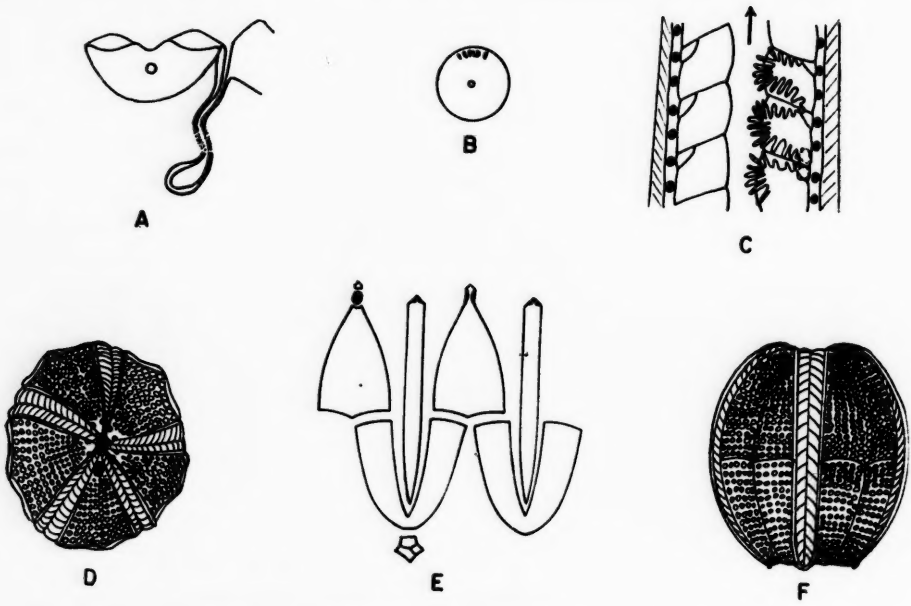
tween an epideltoid and a hypodeltoid plate. One hydrospire fold is present on each side of an ambulacrum, ending in a hydrospire plate along the margins of the deltoid and radial plates. Hydrospire pores are present between the hydrospire plate and the adjacent walls of the radial and deltoid plates. The deltoid plates are almost one-half the length of the calyx. The ambulacra are narrow, linear, with the middle one-fourth (outer surface) of the lancet plate exposed, with primary and secondary side plates covering the margins of the lancet. Basal plates small, in depressed concavity at aboral extremity of calyx.

This genus occurs in the Warsaw limestone of the Meramecian series but may extend into the Keokuk and Burlington limestones of the Osagian series, pending further investigation.

This genus is closely related to *Cryptoblastus*, but differs in three main aspects. In *Cryptoblastus* there are two hydrospire folds along the margin of each ambulacrum, the hydrospire plate is absent along the margin of the deltoid, and the deltoids are short. *Orbitremites* has five spiraculate openings, composed of four spiracles and an anispiracle, whereas *Ptychoblastus* has nine spiraculate openings, composed of eight spiracles and an anispiracle. *Orbitremites* lacks a hydrospire plate along margins of the deltoids. *Mesoblastus* has five paired spiracles, with the posterior spiracle partially fused with the anal opening, but with no hydrospire plate along the deltoid margins. *Acentrotremites* has ten separate spiracles with the anal opening separate. The above mentioned blastoids are all the described elliptical-shaped spiraculate blastoids that contain a hydrospire plate to which *Ptychoblastus* may be related, and not one of these genera include all the features of *Ptychoblastus*. *Ptychoblastus* was probably derived from *Cryptoblastus*.

PTYCHOBLASTUS PUSTULOSUS Fay, n. sp.
Text-fig. 1, A–F

The calyx is 8–12 mm. high, 6–8 mm. wide, and elliptical shaped, with the greatest width near the middle. The deltoids extend to almost one-half the height of the calyx, with two small spiracles notched in the lateral margins of each deltoid near the adoral tip, except on the posterior side. On the posterior side there are two deltoid plates: an epideltoid, between the anal opening and the oral opening, with concealed spiraculate openings on either side that fuse with the anal opening externally; and a hypodeltoid that extends from the anal opening to the radial plates, being almost equal in size to the other four deltoid plates. The radials are about one-half the height of the calyx, sharply rounded aborally into the concave base. The basal concavity is 1–2 mm. wide, with three normally disposed basal plates. Ambulacra are linear, extending the height of the calyx, with a hydrospire plate along each margin between the adjacent radial and deltoid plates. Hydrospire pores are present between the hydrospire plate and adjacent radials and deltoids, each alternating pore apparently spaced evenly with each brachiolar socket. The ambulacra are about 1 mm. wide and contain approximately three primary side plates per millimeter in length. The Lancet plate in cross-section is convex inward at the base, grooved in the middle fourth of the outer surface to form the main food groove, with a central canal below the food groove. The lancet plate and side plates are bordered by the hydrospire plates. One hydrospire fold is present on each side of an ambulacrum, formed from infolds of the adjacent radial and deltoid plates. The primary side plates are broadly trapezoidal, each one extending about three-eighths the width of the lancet plate, with a raised ridge on the admedial half of each plate. The side food grooves extend about one-half the length of a primary side plate, with about five cover plate sockets on each side of a groove. The brachiolar facet is divided into two parts, with one attachment scar on a primary side plate and the other scar on the adjacent adoral secondary side plate. The secondary side plate, termed outer side plate by many authors, is broadly triangular in outer view, resting on the adoral bevelled edge of the side plate limb, with straight adlateral and adoral margins but a curved aboral margin, closely resembling one-eighth of a sphere (Text-figure 1,C.). This type of arrangement suggests that the secondary side plate func-



TEXT-FIG. *1*—*Ptychoblastus pustulosus* Fay, *n. gen.* and *n. sp.*

A. Cross-section through lancet and deltoid plate showing hydrospire plate and one hydrospire fold, ×13, paratype 3644.
B. Stem impression on basal plates showing crenellae on one portion, ×13, paratype 3645.
C. Surface view of an ambulacrum in detail along deltoid margins, with arrow pointing toward oral opening, ×13, paratype 3645.
D. Oral view showing eight spiracles and anispiracle, ×3.6, composite.
E. Plate layout showing B and C (rt. ant., rt. post.) radials only, with one normal deltoid between, and the epideltoid and hypodeltoid to the left of C ambulacrum, ×3.6.
F. Left posterior radial view showing shape and elongated deltoids, ×3.6, composite of holotype 3643 and paratypes 3645.

tioned as a flexible support for a brachiole, allowing the aboral portion of the brachiole to move. The surfaces of well preserved specimens are covered with coarse granules or pustules, arranged along growth lines, with about four pustules per millimeter. The stem is round, with about 40 crenellae near the margin, about ½ mm. in size.

Remarks.—The name of this species is derived from the Greek word for fold, referring to the one hydrospire fold on each side of an ambulacrum, ending marginally in a hydrospire plate. The trivial name refers to the pustulate ornamentation. This species is closely related to *Granatocrinus excavatus* Rowley & Hare 1891 and *Cryptoblastus granulosus* (Meek & Worthen) 1865 reported from the Keokuk limestone, Pike County, Missouri, by Rowley (1908). The former species may belong to *Ptychoblastus*, differing from *P. pustulosus* in size and shape. The deltoid plates of *Granatocrinus excavatus* have slight coronal processes and this species is twice the size of *P. pustulosus*. The former occurs in the Keokuk limestone and the latter in the Warsaw limestone. *Cryptoblastus granulosus* occurs in the Keokuk limestone of Illinois and Missouri, and in the upper part of the Burlington limestone of Missouri and Iowa according to Cline (1937, p. 645). Cline reports that this species has pores marginal to the deltoids along the ambulacra, but that they are not bordered by a hydrospire plate and that there are two hydrospire folds on each side of an ambulacrum. Thus *Cryptoblastus granulosus* could have given rise to *Ptychoblastus pustulosus* if the marginal edge of the hydrospire

fold along the deltoids thickened and grew outward between the lancet and deltoid plate and the two hydrospire folds of *Cryptoblastus granulosus* atrophied to one fold. Moore (1928, p. 248) reports *Cryptoblastus granulosus* from the Warsaw limestone, and it is possible that the reported Warsaw occurrences of this species may be referred to *Ptychoblastus*. The type for *Cryptoblastus granulosus* has not been restudied and occurs in the Keokuk limestone of Illinois. The specimens studied by Cline (1937) occur in the upper part of the Burlington limestone and it is possible that *Cryptoblastus granulosus* may be restricted to the Keokuk and upper part of the Burlington limestones.

Types.—Holotype, 3643; paratypes, 3644, thin-section, and 3645, six specimens and one thin-section with fragment; Geology Department, University of Oklahoma, Norman, Oklahoma.

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JOURNAL OF PALEONTOLOGY, V. 34, NO. 6, P. 1202–1206, 1 TEXT-FIG., NOVEMBER, 1960

CONODONTS FROM THE GLEN DEAN FORMATION OF KENTUCKY AND EQUIVALENT FORMATIONS OF VIRGINIA AND WEST VIRGINIA

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INTRODUCTION

THE conodont fauna of the Glen Dean Formation (Chester) is known to be uniform in composition and distribution throughout the Illinois Basin (Rexroad, 1958). This uniformity over broad areas and in varying lithologies for a given time unit seems to be characteristic of conodonts. However, virtually no conodont occurrences have been described from a geosynclinal environment, and no study has been made to relate shelf and geosynclinal occurrences. The study of such relationships is the primary purpose of this investigation.

The Glen Dean Formation and its correlatives in eastern Kentucky, Virginia, and West Virginia were chosen for study because: (1) correlations of the units are well established and time equivalency of the various units is reasonably assured; (2) the Glen Dean Formation in the Illinois Basin was known to contain an abundant conodont fauna; and (3) the units provide sections extending from the shelf area eastward into the geosyncline with marked changes in lithology and thickness and so are preferred units for biofacies analyses.

Furthermore, it was hoped that studies of Glen Dean age conodonts outside the Illinois Basin would develop new stratigraphic information. There is a minor geographic variation in the Glen Dean conodont fauna in the southern part of the Illinois Basin which seems to indicate closer affinities with the Delaware Creek Member of the Caney Shale of Oklahoma and the Barnett Formation of Texas than does the remainder of the Glen Dean fauna. If this and future studies were to show a group of fossils characteristic of and limited to Glen Dean time (an assemblage-zone), this would be of great value for precise correlations to the standard section of the Mississippian.

Six sections were chosen for study. Their locations are shown in Text-figure 1. Localities 1 and 2 are in the eastern Kentucky shelf area; localities 3, 4, 5, and 6 are in the geosyncline with the last three located approximately along the strike. These last three show a lateral variation from limestone in the southwest at locality 4 to dominantly shale northeast at locality 6.

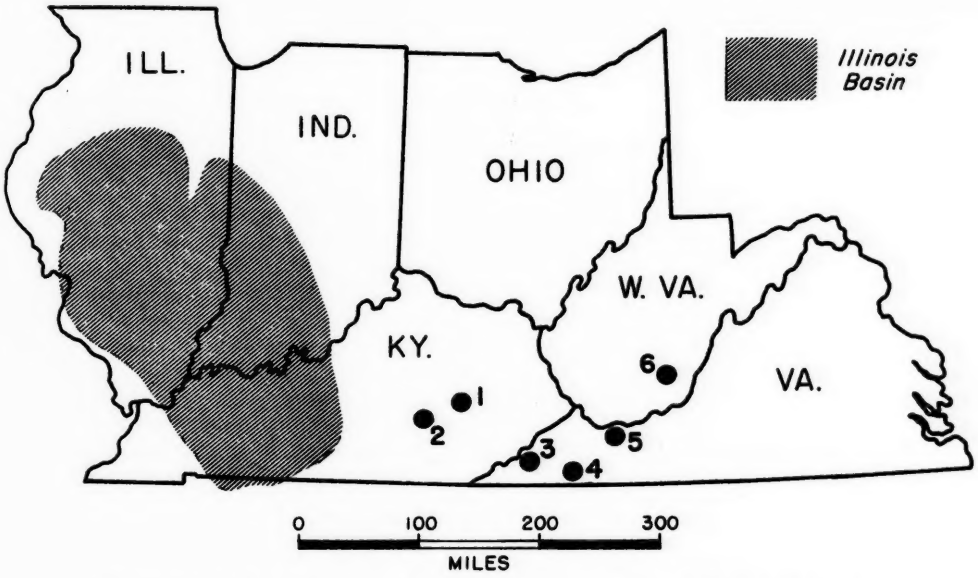
ACKNOWLEDGMENTS

This study is an Illinois State Geological Survey project in cooperation with the Geology Departments of Texas Technological College and the University of Houston. D. H. Swann collected the samples at locality 1, gave advice on stratigraphic aspects throughout the study, and critically read the manuscript. G. H. Emrich assisted the senior author in collecting from the other localities. Charles Collinson and H. B. Willman criticized the manuscript. Marie Litterer prepared the text figure. All are with the Illinois State Geological Survey. Publication is authorized by the Chief, Illinois State Geological Survey.

STRATIGRAPHIC SUMMARY

The Glen Dean Formation, the Cove Creek Limestone, the Bluefield Shale, and the Bluefield Group are all considered to be essentially correlative (Weller *et al.*, 1948). Collections from localities 1 and 2 are from the Glen Dean Formation, which was named by Butts (1917) for outcrops in Breckenridge County, Kentucky. Collections from localities 3 and 5 are from the Bluefield Shale named by Campbell (1896) from Mercer County, West Virginia, and the Bluefield Group is represented at locality 6. The Cove Creek Limestone, named by Butts (1940) from Scott County, Virginia, is exposed at locality 4.

In eastern Kentucky the Glen Dean Formation overlies with apparent conformity the Hardinsburg ("Pencil Cave") Shale and in turn is overlain unconformably by the Pennsylvanian sediments of the Pottsville



TEXT-FIG. 1—Localities from which conodonts were collected. See "Register of Localities" for references to published descriptions of the sections.

Series. In western Virginia and West Virginia the correlative units overlie the Greenbrier or Gasper Limestones except at locality 4 where the Fido Sandstone lies between the Gasper and Cove Creek Limestones. Conformably overlying the Glen Dean correlatives is the Stoney Gap Sandstone Member of the Pennington Formation.

THE CONODONT FAUNA

Although approximately 1,850 specimens were recovered from the six sections sampled, less than one-third of them are generically identifiable, exclusive of fragments of the long ranging genus *Hindeodella*. Twenty-seven named species distributed among thirteen genera, including *Hindeodella*, are represented. These genera are: *Cavusgnathus*, *Cladognathodus*, *Geniculatus*, *Gnathodus*, *Hibbardella*, *Hindeodella*, *Lambdagnathus*, *Ligonodina*, *Lonchodina*, *Neoprioniodus*, *Ozarkodina*, *Roundya*, and *Spathognathodus*. Genera and species, none new, and their distribution are detailed in Table 1.

Additionally, single specimens of *Metalonchodina*, *Synprioniodina*, and *Icriodus* and two specimens of *Polygnathus* were found. Reworking for the last two genera seems evident and is probably the case for *Synprioniodina*. However, evidence for reworking is difficult to assess. At any rate, stratigraphic interpretations based on only one or two specimens should be avoided.

The most abundant species is *Cavusgnathus unicornis* Youngquist & Miller. The second most common is *Neoprioniodus scitulus* (Branson & Mehl). Species considered to be common in order of decreasing numbers are: *Ligonodina hamata* Rexroad, *Cavusgnathus convexa* Rexroad, *Gnathodus commutatus* (Branson & Mehl), *Gnathodus bilineatus* (Roundy), *Cavusgnathus cristata* Branson & Mehl, *Ligonodina obunca* Rexroad, *Neoprioniodus varians* (Branson & Mehl), *Spathognathodus cristula* Youngquist & Miller, and *Hibbardella milleri* Rexroad.

The collection is reposited at the Illinois State Geological Survey under the numbers 14P1–14P155.

ENVIRONMENTAL SIGNIFICANCE OF THE FAUNA

The number of independent variables relating to environment precludes mathematically precise conclusions. However, a number of general conclusions seem warranted from data relating to lithologic variation, differences in thickness, geographic location, and distribution in relation to tectonic setting.

The distribution of species within the area studied is quite uniform. Irregularities in distribution probably result from random sample variation rather than environmental factors or geographic position. It should be noted that this fauna is very similar to that of rocks of the same age in the Illinois Basin, which further indicates geographic uniformity in distribution of conodonts.

On the other hand, abundance of the conodonts varies markedly in differing lithologies and with the thickness of the sections involved. Conodonts are markedly more abundant in limestones than shales, both in the numbers of specimens produced and in the percentage of samples that yielded conodonts. Overall, one out of two limestone samples produced conodonts, but only one out of six shale samples were productive. Excluding locality 4, six out of seven limestone samples produced conodonts. At locality 4, one in six shale samples produced conodonts. The difference between the number of specimens per sample for limestone as opposed to shale samples is even more marked than the difference in the number of producing samples. Because of the relative sparsity of conodonts from shales, many species were recorded only from limestone. In general, there is an inverse relation between thickness of the sections and the abundance of specimens.

It may be possible that the differences in abundance result from variations in the rate of sedimentation as suggested by Collinson, Rexroad & Scott (1959, p. 696). In favorable environments the numbers of conodont-bearing animals may have remained relatively constant, but in the more rapidly accumulating sediments, such as the shales, there would be fewer conodonts per unit sample than in the more slowly accumulating limestones. This concept can not be mathematically demonstrated, but the present study does show the geosynclinal environment to be as favorable for conodonts as that of shelf and intracratonic basin areas.

STRATIGRAPHIC IMPLICATIONS OF THE FAUNA

On the occurrence chart (Table I) the columns on the right are devoted to a comparison of the genera and species of this report with those of the Glen Dean Formation in the Illinois Basin, the Pella Beds of Iowa, the Delaware Creek Member of the Caney Shale of Oklahoma, and the upper conodont zone of the Barnett Formation of Texas.

As would be expected, the composition of the conodont fauna in the area of study is nearly identical with that of the Glen Dean Formation of the Illinois Basin. The differences show that the present fauna has somewhat closer affinities to the Barnett and Caney faunas than does that of the Glen Dean of the Illinois Basin. Although the fauna of the Pella Beds of Iowa is not yet well known, it is closely similar to the Chester of the Illinois Basin and to the fauna of this study.

All genera of the Illinois Basin Glen Dean were represented in this area and only two additional genera have been found. They are *Metalonchodina* and *Geniculatus*, represented by one and two specimens respectively. Both genera have been recorded from the upper conodont zone of the Barnett Formation of Texas and the Delaware Creek Member of the Caney Shale of Oklahoma.

Three species not recorded in the Illinois Basin were found in this study. *Neoprioniodus ligo* (Hass) and *N. singularis* (Hass) are known from both the Barnett and Caney faunas, as is *Gnathodus bilineatus* (Roundy), if one follows Hass (1953, p. 78) in placing *Gnathodus pustulosus* Branson & Mehl in synonomy with the former. Four species from the Glen Dean of the Illinois Basin were not recorded in this area. *Neoprioniodus camurus* Rexroad and *Ozarkodina compressa* Rexroad are common in the basin, but fragments of *Ozarkodina* are very difficult to place. This probably accounts for the latter not being recognized here. *Cladognathodus mehli* (Rexroad) and *Lambdagnathus fragilidens* Rexroad are uncommon in the Illinois Basin.

The ten genera described by Hass (1953) as indigenous to the Barnett are all present in the Glen Dean and its correlatives. However, the Glen Dean units contain four genera not recorded from the Barnett Formation. These are *Cladognathodus*, *Hibbardella*, *Lambdagnathus*, and *Spathognathodus*. Of the twenty-seven species of this report and the nineteen of the Barnett, twelve are common to both. It should be noted in this connection that the Barnett Formation represents a much longer time

TABLE 1—GEOGRAPHIC OCCURRENCE OF CONODONT SPECIES. LOCALITY NUMBERS ARE THOSE USED IN THE "REGISTER OF LOCALITIES"

Locality	1	2	3	4	5	6	Glen Dean Formation, Illinois Basin	Pella Beds	Caney Shale	Barnett Formation
Cavusgnathus	x	x	x	x	x	x	x	x	x	x
C. convexa	x	x	x	–	x	x	x	1	–	–
C. cristata	x	x	x	–	x	x	x	–	x	x
C. regularis	–	x	x	–	x	x	x	x	–	–
C. unicornis	x	x	x	x	x	x	x	x	–	–
Cladognathodus	x	–	x	–	–	x	x	–	–	–
C. prima	–	–	x	–	–	–	x	–	–	–
Geniculatus	–	x	–	x	–	–	–	–	x	x
G. cf. *claviger*	–	x	–	x	–	–	–	–	x	x
Gnathodus	x	x	x	x	x	x	x	x	x	x
G. bilineatus	x	x	x	x	x	–	–	–	–	x
G. commutatus	–	–	x	x	x	–	x	x	x	x
G. modocensis	–	–	–	–	x	–	x	1	x	–
Hibbardella	x	x	x	–	–	x	x	1	x	–
H. milleri	x	x	x	–	–	x	x	1	1	–
H. ortha	–	x	x	–	–	–	x	1	1	–
Hindeodella	x	x	x	x	x	x	x	x	x	x
H. undata	–	x	x	–	–	–	x	–	x	x
Lambdagnathus	–	x	x	–	–	–	x	–	–	–
Ligonodina	x	x	x	x	x	x	x	x	x	x
L. hamata	x	x	x	x	–	x	x	x	–	–
L. obunca	x	x	x	x	x	x	x	x	–	–
L. roundyi	–	–	–	–	x	–	x	–	–	x
Lonchodina	x	x	x	x	x	x	x	–	x	x
L. furnishi	–	–	x	–	x	–	x	–	–	–
L. cf. *paraclarki*	x	x	–	–	–	x	x	–	1	x
L. cf. *paraclaviger*	–	–	–	x	–	x	x	–	1	1
Metalonchodina	–	x	–	–	–	–	–	–	x	x
Neoprioniodus	x	x	x	x	x	x	x	x	x	x
N. ligo	–	–	x	–	–	–	–	–	1	x
N. loxus	–	–	–	x	x	–	x	1	–	–
N. scitulus	x	x	x	–	x	x	x	–	x	x
N. singularis	–	–	–	x	x	–	–	1	1	x
N. varians	x	x	x	–	–	x	x	–	x	–
Ozarkodina	–	x	x	x	x	–	x	–	x	x
O. curvata	–	–	x	x	–	–	x	1	–	–
Roundya	x	x	–	x	–	–	x	–	1	x
P. barnettana (*R. costata*)	x	x	–	–	–	–	x	–	1	x
Spathognathodus	x	x	x	x	x	x	x	x	x	–
S. campbelli	–	–	–	–	x	–	x	–	1	–
S. cristula	x	x	x	x	x	x	x	x	–	–
S. spiculus	–	–	x	–	–	–	x	x	–	–

1, Identification based on author's collections.

interval than does the Glen Dean (Defandorf, 1960).

All twelve genera from the Delaware Creek Member of the Caney Shale are represented in the present material, but two genera from the Glen Dean units have not been reported in the Caney Shale. These are *Cladognathodus* and *Lambdagnathus*. Fourteen of eighteen Delaware Creek species are represented in this study.

It is suggested that the difference in the faunas of the present study, the Illinois Basin Glen Dean, the *Gnathodus bilineatus* zone (Defandorf, 1960) of the Barnett Formation of Texas, and the Delaware Creek Member of the Caney Shale is primarily one of geographic province rather than a time disparity. The Illinois Basin represents one faunal province, the indicated portions of the Barnett and Caney represent another, and the area of this study shows commingling of the two. There is no evidence of any middle Mississippian elements in the parts of either the Caney or Barnett as mentioned above. *Streptognathodus*, which may be as old as very uppermost Chester but is commonly considered Pennsylvanian, is present in the upper part of the Sand Branch Member of the Caney Shale (Elias, 1956, p. 120) and in beds considered to belong with the Barnett (Defandorf, 1960). Accordingly, the Delaware Creek Member of the Caney and the *Gnathodus bilineatus* zone of the Barnett must be considered of Chester age with the possibility that they may also represent deposition into the Pennsylvanian.

REGISTER OF LOCALITIES

Locality 1.—Yellow Rock. Kentucky Stone Company Quarry approximately six miles west of Beatyville along Louisville and Nashville Railroad. Heidelberg Quadrangle, Lee County, Kentucky (McFarlan & Walker, 1956, pl. 2 and p. 25).

Locality 2.—Pine Hill. Approximately six miles south of U. S. Highway 25 at Pine Hill, Mt. Vernon Quadrangle, Rockcastle County Kentucky (McFarlan & Walker, 1956, pl. 2, and p. 18).

Locality 3.—Big Stone Gap. Along Southern Railroad in gap of Powell River through Little Stone Mountain approximately 0.75 of a mile north of Big Stone Gap, Big Stone Gap Quadrangle, Wise County, Virginia (Wilpolt & Marden, 1949, sheet 2; Butts, 1917, p. 386).

Locality 4.—Greendale. Along U. S. Highway 19 from approximately one mile to approximately 0.5 of a mile northwest of Greendale, Brumley Quadrangle, Washington County, Virginia (Butts, 1940, p. 389).

Locality 5.—Bishop. Along Virginia Highway 16 starting approximately 0.6 of a mile southeast of Bishop (Shraders), Pounding Mill Quadrangle, Tazewell County, Virginia (Wilpolt & Marden, 1949, sheets 2, 3).

Locality 6.—Alta. Along U. S. Highway 60 approximately 1.5 miles west of Alta, Clintonville Quadrangle, Greenbrier County, West Virginia (Price & Heck, 1939, p. 181).

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PLIOCENE FRESH-WATER GASTROPODS FROM SAN MATEO COUNTY, CALIFORNIA

WILLIAM GLEN
San Mateo, California

ABSTRACT—*Parapholyx durhami* and *Fluminicola sanmateoensis*, both new species, are described from a new locality in the fresh water upper Pliocene? Santa Clara formation in north-central San Mateo County, California.

INTRODUCTION

RECENT excavations in a quarry on the San Francisco Peninsula at the northernmost mapped extent of the Santa Clara Formation have exposed a new locality which has yielded well preserved univalves intimately associated with fossil wood, including a cone of *Pinus insignus* (=*Pinus radiata* Don.). The faunule is composed exclusively of *Fluminicola sanmateoensis* and the more abundant and generally better preserved *Parapholyx durhami*.

G. Dallas Hanna generously photographed the type specimens at the California Academy of Sciences, and offered helpful suggestions. Allyn Smith also criticized the manuscript, Leo G. Hertlein of the Academy and A. Myra Keen of Stanford University kindly supplied material for comparison from the collections of their respective institutions.

Savage (1951) recently reviewed the history of the term "Santa Clara" and concluded that strata of many different modes of origin, lithologic types, and ages are now referred to the Santa Clara Formation. This results in a nomenclatural problem which should be resolved by the establishment of a type section and locality. Savage states that Louderback (oral communication) had remarked that Branner and his associates considered the vertebrate bearing beds at Irvington to belong to the Santa Clara. The Irvington fauna (southern Alameda County, California) is presently considered to be middle Pleistocene in age (oral communication, R. A. Stirton, 1959).

Lawson (1893) was the first to note fresh water sediments in the Santa Clara Valley. Cooper (1894) placed the "Santa Clara Lake beds" in the Pliocene on the basis of a molluscan fauna consisting of two living and six extinct species (all but two are presently considered Pliocene or older). Branner *et al.* (1909) designated the same beds late Pliocene-early Pleistocene. Hannibal (1912) referred the Santa Clara to the Pliocene in a discussion of Californian faunas. He noted that the faunas of the Kettleman (southern San Joaquin Valley, California), Santa Clara, and Cache (Idaho) Formations are composed of half or more living species, that represent the existing Californian fauna "in nearly its present form." These faunas supposedly indicate the introduction of subboreal conditions with extensive lakes.

The montane aspect of the Santa Clara floral elements led Dorf (1930) to postulate humid conditions with a general cooling (of unknown geographic extent) in the upper Pliocene; seventeen recorded plant species, representing only living genera suggested an upper Pliocene age.

It appears that a questionable upper Pliocene age for the Santa Clara is in keeping with available evidence.

OCCURRENCE

The fossil material described herein was collected from California Academy of Sciences locality number 36724, San Mateo Quadrangle, California, 7½ minute series; U. S. Geol. Survey, San Mateo County; T. 5 S., R. 5 W., 300 yards north, 45° west of the entrance (on Skyline Blvd.) to the Skyline Materials Plant No. 1. Fossils were collected from a clearly exposed cut in which the basal one to two feet thick, lignitic light to dark gray poorly indurated and highly fossiliferous mudstone stratum of the Santa Clara rests with angular unconformity on the highly brecciated Cretaceous Calera limestone member of the Franciscan formation. The stratum is overlain by characteristic Santa Clara gravels which merge indistinguishably with the overlying alluvium. The

lignitic mudstone bed, fossiliferous throughout its exposed lateral extent of 50 feet, dips approximately 9° northwesterly along most of the cut but is sharply downflexed to a 20° dip at the northern end of the cliff face. The presently described locality is situated several miles north of previously reported Santa Clara fossil localities.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA

Family AMNICOLIDAE

FLUMINICOLA SANMATEOENSIS Glen, n. sp.

Text-figs. 1E–1G

Representatives of this species are small compared to other members of the genus. They possess a relatively thick shell wall that is smooth with the exception of barely visible growth lines on the body whorl. The spires are variable in height and have 3.5 to 4.5 whorls. The shell is nonumbilicate, but lacunae adjacent to the columella simulate an umbilical chink that extends almost half way from the base to the first suture. The parietal and columellar lips are thickly calloused; the peristome is continuous and the columellar portion is appressed to the last whorl. The whorls are generally slightly swollen below the suture and range in outline from subcarinate to well rounded. The sutures are deeply impressed. The aperture is oblique and weakly angulate posteriorly.

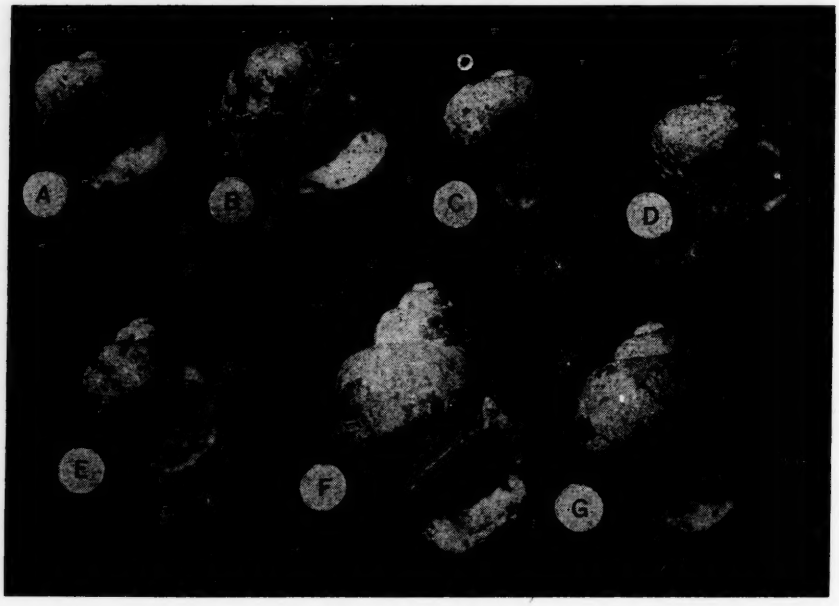
Measurements.—Holotype: length 4.80 mm., width 3.75 mm., aperture length 2.85 mm., aperture width 1.80 mm.

Holotype.—Calif. Acad. Sci. 10449.

Paratypes.—Calif. Acad. Sci. 10450, Univ. Calif. Mus. Paleontology 30093.

Remarks.—This species differs from *F. malheurensis* Henderson & Rodeck from the Pliocene near Vale, Oregon, in its slightly higher spire, broader shoulders, posteriorly less sharply angulated aperture and the presence of a columellar lacuna.

The description and figures of *F. yatesiana* (Cooper) by Pilsbry (1935, p. 553, pl. 20, figs. 8–11) show a wide range of variation in many characters, especially spire height, aperture size and shape, development of peripheral carinae and umbilical character which varies from very narrow to closed. Hannibal (1912) reported that both rounded and peripherally carinate individuals were included in the species *F. yatesiana* and that all specimens were umbilicate; in contradistinction to both Pilsbry's and Hannibal's



TEXT-FIG. 1—Apertural views of *Paraphyolyx durhami* Glen, n. sp., and *Fluminicola sanmateoensis* Glen, n. sp., all ×6. *A–D, Parapholyx durhami* Glen, n. sp. *A*, holotype CAS 10451; *B*, paratype CAS 10451A; *C*, paratype UCMP 32763; *D*, paratype UCMP 32124. *E–G, Fluminicola sanmateoensis* Glen, n. sp. *E*, paratype CAS 10450; *F*, paratype UCMP 30093; *G*, holotype, CAS 10449.

descriptions. *F. sanmateoensis* is not umbilicate.

Fluminicola williamsi (Hannibal) (Hannibal, 1912, p. 189, pl. 8, fig. 29a; Pilsbry, 1935, p. 551, pl. 19, figs. 5–7) differs from *F. sanmateoensis* in its open umbilicus, less deeply impressed sutures. generally smaller size, and thinner shell.

Family PLANORBIDAE
Genus PARAPHOLAX Hanna
PARAPHOLYX DURHAMI Glen, n. sp.
Text-figs. 1A–1D

Members of this species are relatively small and the shell wall is extremely thick. There are three whorls. They are slightly adpressed against the sutures which are impressed. Growth lines are well developed on the ultimate whorl but are barely visible on other whorls. The aperture ranges in shape from subcircular to oval and is oblique in orientation; the posterior lip of the peristome is applied to the last whorl well below the periphery. A distinctive, shallow, smoothly curving depression is bounded interiorly by the columella and exteriorly by a sharp ridge which falls away anteriorly to become the anterior apertural lip. The depression extends along the inner lip from a short distance below the suture to the columellar base and gradually diminishes, extending around the anterior lip. The parietal and columellar lips are thick and reflected. The anterior lip is reflected to form an extension of the depression along the inner lip.

Measurements.—Holotype: length 3.00 mm., width 3.10 mm., aperture length 1.85 mm., aperture width 1.65 mm.

Holotype.—Calif. Acad. Sci. 10451.

Paratypes.—Calif. Acad. Sci. 10451A, Univ. Calif. Mus. Paleontology 32124 and 32763.

Remarks.—This species is closest to *P. solida* (Dall), known only from the Recent, but is much smaller and differs markedly in the structure of the inner and anterior lip regions. The inner lip region of *P. solida* was described by Dall (1870, p. 335) as having a " . . . prominent rounded ridge outside of the columella and the latter is, so to speak, inside of the aperture of the shell. . . . " This description is suggestive of *P. durhami*, but the pronounced smoothly curving depression or flat along the inner and anterior lip areas formed by thickening and reflection is quite unique and not found in other presently known fossil or living species of the genus. The lip region in *P. durhami* approaches that of the genus *Littorina*, in which the columella is generally excavated or flattened.

Baily & Baily (1951) discuss the history of classification of living forms within the genus; Baker (1945) monographed the genus; Henderson (1936, pl. 1, figs. 5–8) figured and discussed the closely related *P. solida*, *P. effusa nevadensis*, and *P. effusa effusa* and showed a wide morphologic range for those species.

Parapholyx durhami is named for Professor J. Wyatt Durham of the University of California at Berkeley.

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NEW NAME FOR *SPIRIFER OCCIDENTALIS* (GIRTY) AND ITS GEOLOGIC HISTORY

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ABSTRACT—*Spirifer occidentalis* (Girty, 1927) Dunbar & Condra, 1932, is a homonym of *Spirifer occidentalis* Kindle, 1908 and is renamed *Spirifer occiduus*. The earliest known representatives of this species occur in the environs of Millard County, Utah, and this area could be the evolutionary center of the species. *Spirifer occiduus*, of early Pennsylvanian age, probably evolved from a new undescribed species similar to *Spirifer pellaensis* Weller, 1914, of late Mississippian age.

INTRODUCTION

WHILE pursuing studies on the paleontology and stratigraphy of the Mississippian-Pennsylvanian boundary in Utah, the author discovered that some apparently well established species of brachiopods are taxonomically unsound. For example, *Spirifer matheri* Dunbar & Condra, 1932, was proposed without designation of types and *Spirifer occidentalis* (Girty, 1927), one of the most common brachiopods of the lower Pennsylvanian System, requires a new name because *Spirifer occidentalis* was previously applied to a Devonian species by E. M. Kindle in 1908.

ACKNOWLEDGMENTS

The late Merrill A. Stainbrook guided the writer to several topotype localities in Iowa and Illinois. G. G. Huffman and R. L. Langenheim, Jr. sent specimens of particular spiriferids. A. B. Shaw, A. A. Stoyanow, and D. M. Boyd made several specimens available, as did G. A. Cooper, who also acknowledged the availability of the name *occiduus*. R. E. Peck and A. G. Unklesbay loaned several species described by Branson & Greger and Branson. Special thanks are due M. K. Elias for discussing the results of his paleontologic studies in Oklahoma, for permitting access to specimens deposited with the Nebraska Geological Survey, and for obtaining on loan from the University of Chicago the specimens studied by Mather.

SYNONYMY OF *SPIRIFER OCCIDENTALIS*

In 1908 Kindle coined the name *Spirifer occidentalis* for a brachiopod from the Devonian Jefferson Limestone near Princeton, Montana although it now seems unlikely that Kindle's species should be assigned to the genus *Spirifer*. Furthermore, it is not a common species in the Jefferson Formation as it has not been identified or listed by workers after Kindle. Apparently unaware of Kindle's publication, G. H. Girty (*in* Mansfield, 1927, p. 433–434) introduced the name *occidentalis* as a variety of the Pennsylvanian species *Spirifer opimus* Hall, Dunbar & Condra (1932, p. 322–326) elevated the varietal name to specific rank and since 1932 this transverse spiriferid has been known as *Spirifer occidentalis* (Girty)—*occidentalis* from the Latin referring to the western geographic occurrence of the species. Thus, *Spirifer occidentalis* (Girty, 1927) Dunbar & Condra, 1932, is a homonym of *Spirifer occidentalis* Kindle, 1908. This is a violation of article 35 of the rules of zoological nomenclature and *Spirifer occidentalis* (Girty) should be renamed. It is proposed that the shells currently named *Spirifer occidentalis* (Girty) be henceforth known as *Spirifer occiduus*. According to Dr. W. P. Kitaj, professor of languages at Idaho State College, *occiduus* is from the Latin and is used in the poetic sense meaning western. Thus, the proposed name still retains the western connotation.

Girty based the description of this species mainly on three cotypes. The specimen illustrated in U. S. Geological Survey Professional Paper 152 on plate 17, figures 28 and 29 is the best preserved and is designated the holotype, and the other two illustrated specimens are designated paratypes. It should be mentioned that all three types are

somewhat flattened due to compaction after burial, etc. The types were collected from the Wells Formation in sec. 35, T. 9 S., R. 45 E., Crow Creek Quadrangle, Idaho.

Although Girty considered *Spirifer occiduus* a variety of *Spirifer opimus*, the author is of the opinion that the two species represent two separate phylogenetic lineages and that the similarity is due to convergence (Haas & Simpson, 1946). The hypothesis presented is that *Spirifer leidyi* of Chester age evolved into *Spirifer opimus* and that a form of the *Spirifer pellaensis* group or lineage was the ancestor of *Spirifer occiduus*. Due to the variation in width of the shells of *Spirifer opimus* and *S. occiduus* these species have a tendency to look alike; hence, they can be considered isochronous homoeomorphs.

Most of the shells of *Spirifer occiduus* possess a more transverse outline than those of *S. opimus*. The degree of transversity varies according to the number of lateral plicae which commonly averages about 12, but ranges from at least 10 to 15. The number of lateral plicae present partly depends on the number of bifurcated plications and the character of the cardinal extremities; some specimens are alate. Specimens having about 11 lateral plicae are difficult to distinguish from *Spirifer opimus* which typically has about 9 or 10 lateral plications. Fortunately there are limited intermediate specimens, as the populations of both species fit a normal bell-shaped curve in distribution.

SPIRIFER LEIDYI-SPIRIFER OPIMUS TRANSITION

The specimens described as *Spirifer welleri* (Branson & Greger, 1918), especially figure 10 on plate 18, from the "Amsden Formation" of Wyoming are herein considered very late forms of *Spirifer leidyi* and precursors of *Spirifer opimus*. The similarity between *Spirifer leidyi* and *Spirifer opimus* can best be observed when the two species are compared side by side. *Spirifer leidyi*, however, typically has more angular plications, a somewhat deep, angular median groove on the fold, and is smaller than *S. opimus*, whose plications are more rounded. The "Amsden" specimens, considered transitional between the two species, possess rounded plications, the median groove on the fold, are smaller than specimens of *Spirifer opimus*, and have somewhat rounded cardinal extremities which are typically angular in *Spirifer leidyi*.

The age of the so-called Amsden Formation of central Wyoming has been the subject of much controversy. Based on his studies in the more nearly complete stratigraphic and paleontologic Carboniferous section of western and central Utah, the writer considers the fauna described by Branson & Greger (1918), and Burk (1954) as correlative with the upper portion of the Manning Canyon and Chainman Formations of Utah (Sadlick, 1955, p. 56). These beds can be considered either very late Mississippian or early Pennsylvanian. The term *proemial* seems most fitting to describe strata possessing fauna of two geologic ages. Mather (1915, p. 67) credits J. M. Clarke for introducing the term, "an introductory fauna which heralds the incoming of a new organic association and passes gradually, without interval or interruption, into that culminant assemblage." The concluded age determination of the "Amsden" is in part verified by a somewhat crushed goniatite, *Cravenoceras*, exhibiting coarse ornamentation similar to *Cravenoceras scotti* Miller & Youngquist of the late Mississippian Barnett Formation of central Texas. The "Amsden" *Cravenoceras*, which occurs in float 60 to 90 feet above the Madison Limestone, was listed by Burk (1954, p. 7) as an unidentified goniatite. A columnar section at this locality was presented by Shaw & Bell (1955, p. 334).

Exactly how and where *Spirifer leidyi* gave rise to *S. opimus* could be debated. However, the distribution of these two species in western states indicates that *Spirifer opimus* is most common in early Pennsylvanian formations in northeastern Utah. *Spirifer leidyi* is best represented in Alberta, Canada, south-central Montana and adjacent parts of Wyoming, and less so in northern Utah; it is not known or is very rare in western Utah. This chronologic distribution suggests events in the following probable sequence: dominant populations of *Spirifer leidyi* gradually shifted southward from central Montana and Wyoming into the present Uinta Mountain area of Utah. As this geographical and chronological shift (or migration) progressed, so did the evolution

of these spiriferids: *Spirifer leidyi* during Chester time in Montana; later Chester time in Wyoming with advanced forms of *Spirifer leidyi* and precursors of *S. opimus* (*Spirifer welleri*); and finally *Spirifer opimus* in early Pennsylvanian time in northeastern Utah.

Regardless of the correctness of this hypothesis, *Spirifer opimus* is a cryptogenetic form (Jeletzky, 1955, p. 490–491; Sadlick, 1957, p. 57–59) in northern Utah.

Since *Spirifer opimus* is rather common not far above the base of the Oquirrh Formation and the Round Valley Limestone near Salt Lake City, it seems logical to conclude that the "Amsden" beds at Cherry Creek, Wind River Mountains, Wyoming, are older than either of these two early Pennsylvanian formations.

The type of *Spirifer opimus* probably is a medial Pennsylvanian form, if it was collected in the northern part of the Mississippi Valley. The locality of Hall's type is unknown, although other fossil species described by Hall at that time are at the American Museum of Natural History (see reference to Hall *in* Whitfield & Hovey, 1901).

SPIRIFER LEIDYI-SPIRIFER MATHERI TRANSITION

The specimens identified as *Spirifer rockymontanus* by Mather (1915) were placed in a new species, *Spirifer matheri*, by Dunbar & Condra (1932, p. 322). However, no types were specifically designated. Although Mather's forms exhibit substantial variation, the specimen figured on plate XII, figures 4a–c, University of Chicago number 16138, is designated as the holotype of *Spirifer matheri;* the other illustrated specimens can be regarded as paratypes.

There is a striking resemblance between the holotype of *Spirifer matheri* and specimens of *Spirifer leidyi.* This resemblance is especially noted on the submature portions of shells in Mather's collection. University of Chicago specimen number 16483, if compared side by side with shells of *Spirifer leidyi*, probably would be placed in that species by most paleontologists, rather than in *Spirifer matheri.*

The specimens identified by Mather as *Spirifer opimus* are somewhat atypical. University of Chicago specimen numbered 16495 exhibits similarity in its early ontogenetic development to *Spirifer leidyi.* Possibly *Spirifer opimus* of Mather is an example of quantum evolution (Simpson, 1952, p. 234–235) in the *leidyi-opimus* transition. However, its stratigraphic position above *Spirifer matheri* precludes this idea. Nevertheless, such atypical specimens of *Spirifer opimus* are present in the lower beds of the Round Valley Limestone in the Uinta Mountains of Utah. Disregarding the principle of homotaxis, one can only suggest that the origin of *Spirifer matheri* preceded that of *Spirifer opimus;* also, based on the mutual occurrence of similar atypical forms of *Spirifer opimus*, one may correlate the basal beds of the Round Valley Limestone to the relevant beds of the type Morrow Series.

Because of a restricted geographic range it seems very likely that *Spirifer matheri* evolved from *Spirifer leidyi* in the Oklahoma-Arkansas area (Table 1).

One of the significant differences between *Spirifer matheri* and *S. leidyi* is that the former has up to three lateral plicae that bifurcate. However, this is a variable characteristic and when there are no bifurcated plicae, it is difficult to separate the two species. The specimens identified as *Spirifer opimus* by Elias (1957, pl. 57, figs. 4,5,6) should be allied more with the *Spirifer leidyi* group rather than *Spirifer opimus.* Compare Elias' figures (*ibid.*) with those of Weller (1914, pl. XLVII, figs. 28,31).

SPIRIFER PELLAENSIS-SPIRIFER OCCIDUUS TRANSITION

There are at least three described species, and one to be described by W. H. Easton, that are basically similar and seemingly belong to the *Spirifer pellaensis-S. occiduus* transition. Collectively, they can be considered to be the *Spirifer pellaensis* group or lineage. The oldest is *Spirifer pellaensis* Weller, the next youngest is *Spirifer arizonensis* Hernon, then *S. pellaensis cavecreekensis* Hernon, *Spirifer c* (a new undescribed species noted by W. H. Easton), and finally *Spirifer occiduus.* Unfortunately, the types of these spiriferids are not as ideally pre-

TABLE 1—DIAGRAM SHOWING THE RELATIONS OF PENNSYLVANIAN SPECIES AND THEIR MISSISSIPPIAN ANCESTORS ACCORDING TO THEIR AREA OF ORIGIN

Area:	Oklahoma	Millard County, Utah	Wyoming
Pennsylvanian:	*Spirifer matheri*	*Spirifer occiduus*	*Spirifer opimus*
Mississippian:	*Spirifer leidyi*	*Spirifer pellaensis* group	*Spirifer leidyi*

served as those of *Spirifer pellaensis*. Furthermore, topotypes of the latter exhibit much variation in size, angularity of the cardinal extremities, thickness, and nature and number of the plicae, especially those of the fold and sinus. Thus attempts to recognize the various species by quantitative methods have not been very fruitful because the nature of the evolutionary process is too complicated to be illustrated by these methods.

Based on the elevated nature of the umbonal region, *Spirifer arizonensis*, *Spirifer pellaensis cavecreekensis*, and *Spirifer c* probably represent a very closely related ascending lineage; *Spirifer occiduus* does not possess that feature. Specimens of *Spirifer c* from the upper part of the Chainman Formation in the environs of Millard County, Utah, occur together with *Spirifer occiduus*. Furthermore, in some of the sample populations of *Spirifer c* from western Utah there are specimens typical of *Spirifer c* and fewer specimens typical of *Spirifer pellaensis* and *S. occiduus*, including a few forms that could be termed transients between the latter two species. The same is true for collections from the Heath Formation of Montana, except that forms similar to *Spirifer occiduus* are usually lacking or are very rare. At present, evidence is not conclusive that *Spirifer occiduus* originated from *Spirifer c* or from one of the variants of that species, such as *Spirifer shoshonensis* Branson and Greger.

While the writer knows of no one's ever having found *Spirifer occiduus* in Montana or Wyoming, that species is well represented in the basal Pennsylvanian limestones of Utah and eastern Nevada and in the uppermost strata of the underlying Chainman Formation of western Utah. Thus, it seems safe to conclude at this time that western Utah and eastern Nevada, particularly the area about Millard County, Utah, is the evolutionary center of *Spirifer occiduus*. The species probably migrated into the midcontinental region of the United States via the Colorado trough, New Mexico, Texas, and Oklahoma.

The geologic range of *Spirifer occiduus* seemingly is entirely early Pennsylvanian, depending in part on the age assignment of the proemial faunal element that occurs with *Spirifer occiduus* in the upper part of the Chainman Formation. The upper limit of the species is approximately the top of the Krebs Group of the Des Moines Series; at least it is rare above strata equivalent to the Krebs Group. In Illinois it has been reported (Wanless, 1958, p. 19) from the Liverpool cyclothem which has equivalents in the Cabaniss Group. It seems that the Krebs-Cabaniss contact is a very significant one paleontologically since *Spirifer* and *Fusulinella* are rarely encountered above it. Also, lirate forms of *Mesolobus* are not known in strata younger than Krebs, and, as a general rule, there is a marked difference in the elevations of the bundled or trifurcated plications of the genus *Neospirifer*. Those above the Krebs-Cabaniss boundary are more highly elevated and the trifurcations begin closer to the beaks than in specimens below the boundary. *Kozlowskia haydenensis* (Girty) is not known above the Krebs-Cabaniss contact.

Spirifer occiduus has finer and lower plicae than those of the *Spirifer pellaensis* group; the plicae are typically about one-third narrower in *Spirifer occiduus*. Also, the plicae of the lateral slopes of *S. occiduus* commonly bifurcate. Some paleontologists believe that the presence or absence of bifurcated lateral plications has some taxonomic significance. Such an interpretation seems untenable because specimens of both types occur in single collections and ap-

parently lived together. If two species are recognized, it would conflict with "Gause's hypothesis" that two species with closely related habits can not exist together in the same ecological niche.

TYPES OF *SPIRIFER ROCKYMONTANUS* MARCOU, 1858

The types of this species are lost and eventually someone will declare neotypes. It is for this reason that the following statements are quoted from an unpublished doctoral dissertation by John A. Young (1945, p. 170–172):

> "The only figure of the accepted holotype of *Spirifer rockymontanus* are those shown by Marcou. The location of the holotype is unknown. The writer found in the de Koninck collection, of the Museum of Comparative Zoology, several specimens labelled in de Koninck's handwriting, '*Spirifer rockymontanii* n. sp.' The locality given was 'Pri du village de Tegeras, Canon de San Antonio, dans le Rocky Mountains du New Mexico,' and the formation was given as the Mountain limestone, . . . This is the locality cited by Marcou from which the types of *S. rockymontanus* were collected. Inasmuch as some of Marcou's fossils were identified by de Koninck (Marcou, p. 32), the writer feels justified in believing the specimens found to be paratypes studied by de Koninck at the time of the description of the new species for Marcou, although they are not the specimens figured, . . ."

Thus attention is directed to the specimens at Harvard College which might serve as neotypes.

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PALEONTOLOGICAL NOTE

MOSASAUR REMAINS FROM THE UPPER CRETACEOUS OF WESTERN AUSTRALIA

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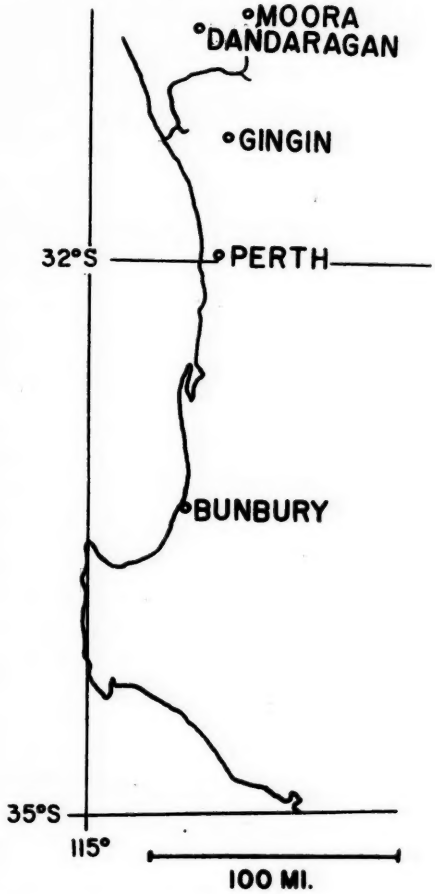
Cretaceous mosasaurs have been recorded from every continent except Australia (Romer, 1945). Their presence in New Zealand and the East Indies indicates that their absence from Australia has been a collecting accident. This note records the first mosasaur fragments from Australia.

The material consists of a left ulna and part of a paddle bone collected from the upper seven feet of the Molecap Greens and (Fairbridge, personal communication) at MacIntyre's Gully near Gingin (31°18′ S, 115°54′ L) Western Australia (Text-fig. 1). Since the stratigraphic position of the remains is known, a brief account of the Cretaceous section and the ages of the units follows.

The Cretaceous section in the Gingin area consists of three units separated from the underlying Jurassic Strathalbyn Sandstone (Fairbridge, 1953) by an angular unconformity (McWhae *et al.*, 1956). The units in order of decreasing age are the Molecap Greensand (Fairbridge, 1953), the Gingin Chalk (Glauert, 1910), and the Poison Hill Greensand (Fairbridge, 1953).

The Strathalbyn Sandstone is composed of siltstone, often micaceous, and sandstones which may be micaceous, ferruginous or both. Walkom (1944) considers its age to be Late Jurassic on the basis of plant fossils. Balme (McWhae, *et al.*, 1956) considers it to be either latest Jurassic or earliest Cretaceous.

The Molecap Greensand is a friable, unbedded, well sorted glauconitic sandstone. It varies from 12 feet at MacIntyre's Gully to 100 feet in bores ¾ miles to the north (Warne, unpublished thesis). Macrofossils are rare in this unit but *Plesiosaurus* sp. and *Ichthyosaurus* sp. bones have been reported from near Dandaragan, and *Pecten* sp. and belemnites have been recorded from the Gingin area (Teichert & Matheson, 1944). Poorly preserved and abraded ammonite remains (probably ceratitic), fish teeth, and fossil wood have since been found (Warne, unpublished thesis). Deflandre & Cookson (1955) consider the age to be late Cretaceous on the basis of microplankton. Fairbridge and Feldtman collected the material described here together with a few pelecypods (Fairbridge, personal communication) from this unit.



TEXT-FIG. 1—Locality map of Western Australia.

The Gingin Chalk appears to lie conformably on the Molecap Greensand. It is composed of a slightly friable, highly fossiliferous chalk which is usually glauconitic. The thickness at the type locality in MacIntyre's Gully is 62 feet. The unit is lenticular and varies in thickness to a maximum of 70 feet (Fairbridge, 1953). It is absent in bores 2½ miles to the north (Warne, unpublished thesis). The age is considered by Withers (1924) to be Santonian on the basis of *Marsupites* and *Uintacrinus*.

The Poison Hill Greensand lies above the Gingin Chalk with apparent conformity. It consists of a friable, glauconitic sandstone with some thin shaly bands. No fossils have been recorded from the Poison Hill Greensand but it is considered to be late Senonian (McWhae, *et al.*, 1958).

The new mosasaur material consists of a left ulna and a paddle bone. The preservation is good except that abrasion has rounded the normally angular ends of the bones.

The ulna is very similar to those of *Platecarpus* and *Clidastes*, perhaps somewhat closer to *Platecarpus*. It is relatively slender, more so than in *Mosasaurus* or any other of the Maestrichtian and Danian forms. Closer identification is not possible because of the abrasion of the ends. This makes unreliable the determination of characters such as the obliquity of the articular surfaces to the main axis which might be used to differentiate these genera.

Williston (1898) gives the age of *Platecarpus* and *Clidastes* in Kansas as upper Turonian and uppermost Turonian or lower Senonian respectively. The part of the Niobrara which contains these genera is now considered to be Santonian in age (Cobban & Reeside, 1952). This is the same age as the Western Australian specimens as determined by invertebrates.

The mosasaurs, being large predators, would be expected to be widespread geographically and useful in the correlation of Cretaceous rocks. However, both Williston (1898) and Camp (1942) state that this is not true. Both these authors state that few genera are widespread and Williston states that two or more distinct types appear suddenly in the Cenomanian and exist together through the upper Cretaceous. This is based on the existence of *Taniwhasaurus oweni* and "*Leiodon*" (*Tylosaurus*) *hamuriensis* from New Zealand. Williston (1898) considered *Taniwhasaurus* to be closely related to, if not congeneric with, *Platecarpus*. A comparison of the figure of the arm of *Taniwhasaurus* given by Hector (1878) with those of other mosasaurs indicates a closer resemblance to the more advanced mosasaurs than to *Platecarpus*. The humerus is greatly shortened; the width is equal to or greater than the length. According to Camp (1942), who has set up a sequence of morphological stages in the evolution of the paddles, this stage in the shortening of the humerus is usually not found until approximately Senonian. Unfortunately the phalanges are not preserved and it is impossible to determine whether they indicate an advanced type of paddle.

There are two possible interpretations of this situation, (1) the advanced characters of the paddle mentioned above arose earlier than suspected but remained restricted geographically until the late Cretaceous, or (2) the Cenomanian age of the New Zealand material is erroneous. Recent studies by Finlay & Marwick (1940) indicate the latter explanation is more likely. They place the age of the unit with the mosasaur remains as Santonian. This removes one of the obstacles (long time span for some types) to their use in correlation. It appears from the above that equivalent morphological types of paddles are of roughly equivalent age.

The other obstacle, that of restricted geographic range, may be more the result of excessive splitting along geographic lines than of actual fact. This has been the situation with the Recent Cetacea. A number of widely distributed species were formerly divided into a number of species based on geographic or individual variants (Norman & Fraser, 1948). It would probably be worthwhile to re-examine the mosasaurs in the light of the modern biological species concept.

The authors are indebted to R. W. Fairbridge, Columbia University for the exact stratigraphic position of the specimens reported here, and to R. T. Prider, University of Western Australia, for arranging the loan of the specimens to one of the authors (E. L.). The authors are also grateful to

Rainer Zangerl for the opportunity of examining the mosasaurs in the Chicago Natural History Museum and to K. P. Young of The University of Texas for information on Cretaceous correlations.

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NOMENCLATURAL NOTE

EMENDATIONS TO UPPER PENNSYLVANIAN ARENACEOUS FORAMINIFERA FROM KANSAS

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Both Hans Thalmann and Brooks Ellis have brought to my attention homonyms for one genus and one species published in 1956.

Bigenerina elongata Ireland, 1956 (Jour. Paleontology, v. 30, p. 862, pl. 7, figs. 15–17, Upper Pennsylvanian of Kansas) is a species preoccupied by *Bigenerina elongata* Gauger, 1953 (Utah Geol. Mineral Survey, Bull. 47, p. 59, pl. 6, figs. 3,4, Upper Cretaceous, Wyoming). *Bigenerina perkinsi* Ireland is the new name to be applied to the species.

Saccamminoides Ireland, 1956 (Jour. Paleontology, v. 30, p. 841, Upper Pennsylvanian of Kansas) is a generic name preoccupied by *Saccamminoides* Geroch, 1955 (Ann. Soc. Geol. Pologne, v. 32, p. 54, Eocene of Czechoslovakia). The new generic name of *Saccamminis* is proposed and the type species should be referred to as *Saccamminis multicella* (Ireland) equals *Saccamminoides multicella* Ireland, 1956. The type species is described in the original paper on p. 841, pl. 3, fig. 2a and 2b. Since publication, additional specimens have been found in the same formation in southern Kansas 200 miles to the south.

I was abroad at the time of publication of the paper and there was no opportunity to check the galley proof without delaying publication of the issue. The final manuscript and the drafting of Text-figure 1 and Table 1 were completed after my departure, and it is unfortunate that inconsistencies between text and figures could not be checked. The following corrections should be noted:

Text-fig. 1. Move locality B-4 south from T. 17 N. to T. 18. N.

Table 1. *Astrorhiza virgilensis:* Move bar from Kereford to Spring Branch.

Thurammina diformens: Move bar from Leavenworth to Plattsmouth, delete Kereford, move bar from Church to Wakarusa.

Tolypammina nodosa: Delete Leavenworth, move Hartford to Ervin Creek.

Textularia bucheri: Move Elmont to Reading.

Bigenerina virgilensis: Add Rock Bluff (common).

Verneuilina virgilensis: Move bar for Kereford to Dubois.

The occurrence of type specimens was given but the locality was omitted from several descriptions and they are given as follows:

p. 841—*Thurammina diformens:* Type is from Coll. A-3; Coll. A-19 should read A-20.

p. 843—*Thurammina lawrencensis:* Type is from Avoca, Coll. B-8.

p. 844—*Thurammina verrucosa:* Type is from Topeka, Coll. A-13.

p. 847—*Glomospira monogranulata:* Holotype is Text-fig. 4-13 and not 4-14.

p. 851—*Tolypammina rugosa:* Type is from Kereford, Coll. B-4.

p. 851—*Ammovertella elevata:* Holotype is from Sheldon, Coll. A-14.

p. 854—*Ammovertella labyrintha:* Type is from Coal Creek, Coll. B-16.

p. 854—*Ammovertella primaparva:* Same as above.

p. 855—*Ammovertella prodigalis:* Type is from Utopia, Coll. A-17.

p. 858—*Ammobaculites parallelus:* Type is from Kereford, Coll. A-4.

p. 859—*Textularia elsiae:* Type is from Rock Bluff, Coll. A-10.

CORRECTION

The following correction should be made in the article, "Devonian Stromatoporoids from the lower Mackenzie Valley of Canada," by J. J. Galloway, Jour. Paleontology, v. 34, no. 4, p. 621, line 39: change LOWER UPPER DEVONIAN, FRASNIAN to UPPER MIDDLE DEVONIAN.

CHARLES COLLINSON, Editor

JOURNAL OF PALEONTOLOGY

INDEX TO VOLUME 34

AUTHOR INDEX

		No.	Page
1.	ADAMS, JOHN K., Note on Lower Tertiary and Upper Cretaceous Ostracoda from New Jersey (Paleontological Note)	2	371
2.	ARNOLD, C. A., The morphology and anatomy of the American species of the genus *Psaronius*. By Jeanne Morgan (Review)	3	602
3.	BANDY, O. L., The geologic significance of coiling ratios in the foraminifer *Globigerina pachyderma* (Ehrenberg)	4	671
4.	BATES, J. D. and BIEMESDERFER, G., Stratigraphy and paleontology of an occurrence of diatomaceous earth in Nebraska (paleontological note)	4	759
5.	BAXTER, JAMES W., *Calcisphaera* from the Salem (Mississippian) limestone in southwestern Illinois	6	1153
6.	BERDAN, JEAN M., Revision of the Ostracode family Beecherellidae and redescription of Ulrich's types of *Beecherella*	3	467
	BERDAN, JEAN M., see SOHN, I. G. (106)		
7.	BERGENHAYN, J. R. M., Cambrian and Ordovician loricates from North America	1	168
8.	BERGQUIST, H. R., Occurrence of Foraminifera and conodonts in Upper Paleozoic and Triassic rocks, northern Alaska (Paleontological Note)	3	596
9.	BERRY, WILLIAM B. N., Early Ludlow graptolites from the Ashland area, Maine	6	1158
10.	BHATIA, S. B. and MANDWAL, N. K., Burdigalian Ostracoda from the Surat-Broach area, western India	2	280
	BIEMESDERFER, G., see BATES, J. D. (4)		
11.	BOLD, W. A. VAN DEN, Note on some species of Ostracoda described by A. M. Norman (Paleontological Note)	3	592
12.	BOUCOT, ARTHUR J., A new Lower Devonian stropheodontid brachiopod	3	483
	BOYD, DONALD R., see MURRAY, GROVER E. (68)		
13.	BROWN, ROLAND W., Corkwood in the Eocene flora of the southeastern U. S.	3	429
14.	BURCKLE, LLOYD H., Some Mississippian fenestrate Bryozoa from central Utah	6	1077
	BURGESS, J. D., see HOARE, R. D. (40)		
15.	BURT, A. M. and WOOD, A. E., Variants among middle Oligocene rodents and lagomorphs	5	957
16.	CAMPBELL, K. S. W., The brachiopod genera *Ingelarella* and *Notospirifer* in the Permian of Queensland	6	1106
	CARRILLO B., JOSÉ, see MURRAY, GROVER E. (69)		
17.	CIFELLI, RICHARD, Variation of English Bathonian Lagenidae and its phylogenetic significance	3	556
18.	CLARK, DAVID L., *Parapuzosia* in the north Texas Cretaceous	2	233
	CLARKE, CHARLES E., see REXROAD, CARL B. (86)		
19.	CONNORS, J. L. and YOCHELSON, E. L., Principles of paleontology—Handbook for paleontologists and geologists of the U.S.S.R.—Y. A. Orlov, Editor (Review)	1	203
20.	COOPER, G. A., Correction of brachiopod names (Nomenclatural Note)	3	601
21.	CRICKMAY, C. H., Studies of the western Canada Stringocephalinae	5	874
22.	CROPP, FREDERICK W., Pennsylvanian spore floras from the Warrior Basin, Mississippi and Alabama	2	359
23.	DOW, V. E., Magnetic separation of conodonts	4	738
24.	EASTON, W. H., Permian corals from Nevada and California	3	570
25.	ESTES, RICHARD, Change of name for a Cretaceous chimaeroid (Nomenclatural Note)	5	1054
26.	ETHINGTON, R. L. and FURNISH, W. M., Upper Ordovician conodonts from southern Manitoba	2	265
27.	FAY, ROBERT O., *Ptychoblastus*, a new Mississippian blastoid from Missouri	6	1198
	FISCHER, A. G., see OSGOOD, R. G. (75)		
28.	FLÜGEL, ERIK, *Heterastridium conglobatum conglobatum* Reuss, an Upper Triassic hydrozoan from the Petra-Tou-Roumiou of Pendakomo, Cyprus	1	127
29.	FOSS, TED H., Structure and composition of associated neurodontiformes and *Astraspis* scales from the Harding formation of Colorado (Paleontological Note)	2	372
30.	FRANKEL, LARRY, Geographic distribution of *Planorbula vulcanata* Leonard in Nebraska (Paleontological Note)	3	591
	FURNISH, W. M., see ETHINGTON, R. L. (26)		

	FURNISH, W. M., see MURRAY, G. E. (69)		
	FURNISH, W. M., see SELLERS, D. H. A. (100)		
31.	GALLOWAY, J. J., Devonian stromatoporoids from the lower Mackenzie Valley of Canada	4	620
32.	GLEN, WILLIAM, Pliocene fresh-water gastropods from San Mateo County, California	6	1207
33.	GORDON, MACKENZIE, JR., Some American midcontinent Carboniferous cephalopods	1	133
34.	GRAHAM, ALAN, Miocene Floras of the Columbia Plateau. Part I. Chaney, Ralph W. Composition and Interpretation. Part II. Chaney, Ralph W., and Axelrod, Daniel I. (Review)	3	603
35.	GRAY, JANE, Fossil chlorophycean algae from the Miocene of Oregon	3	453
36.	GREEN, MORTON, A Tertiary *Cynomys* from South Dakota	3	545
37.	GREEN, MORTON and MARTIN, HAROLD, *Bison latifrons* in South Dakota	3	548
38.	GUTSCHICK, R. C., Photography of Palezoic arenaceous Foraminifera (Paleontologic Note)	4	756
	HATTIN, D. E., see PERRY, T. G. (78)		
39.	HOARE, R. D., New Pennsylvanian Brachiopoda from southwest Missouri	2	217
40.	HOARE, R. D. and BURGESS, J. D., Fauna from the Tensleep Sandstone in Wyoming	4	711
41.	HOFKER, J., The type localities of the Maestrichtian (Maestrichtian chalk tuff) and of the Montian (Tuffeau de Ciply, Calcaire de mons, Lagunar, and Lacustre Montian)	3	584
42.	HOWARTH, M. K., Generic names for Ammonoidea published during the period 1758–1954	1	194
43.	HOWE, H. J., *Turbinolia rosetta*, a new coral species from the Paleocene of Alabama	5	1020
	HU, CHUNG-HUNG, see LOCHMAN, CHRISTINA (61)		
44.	IRELAND, H. A., Emendations to Upper Pennsylvanian arenaceous Foraminifera from Kansas (Nomenclatural Note)	6	1218
45.	JEFFORDS, R. M. and MILLER, T. H., Air brush for whitening fossils, and notes on photography	2	275
46.	JELINEK, A. J., A late Pleistocene vertebrate fauna from Texas	5	933
47.	JOHNSON, J. HARLAN and KONISHI, KENJI, An interesting late Cretaceous calcareous alga from Guatemala	6	1099
	JONES, D. H., see STEVENS, C. H. (109)		
48.	JONES, DAVID L., Lower Cretaceous (Albian) fossils from southwestern Oregon and their paleogeographic significance	1	152
49.	JONES, DAVID L., Pelecypods of the genus *Pterotrigonia* from the west coast of North America	3	433
50.	JUX, ULRICH, *Montecaris lehmanni*, A new crustacean from the Rhenish Devonian and the problem of its systematic position	6	1129
51.	KESLING, R. V., Grundzüge der zoologischen Mikropaläontologie, by Valdimier Pokorný (Review)	1	205
52.	KIER, PORTER M., Cenozoic echinoids of Eastern United States by C. Wythe Cooke (Review)	3	602
53.	KLING, STANLEY A., Permian fusulinids from Guatemala	4	637
54.	KOLOSVÁRY, G., New fossil balanid localities in Hungary (Paleontological Note)	3	590
55.	KOLOSVÁRY, G., The phylogenetic classification of the madreporarian corals (Paleontological Note)	5	1051
	KONISHI, KENJI, see JOHNSON, J. HARLAN (47)		
	KONIZESKI, R., see ROHRER, W. L. (88)		
56.	KORNICKER, LOUIS S., Methods of measuring the internal volume of shells (Paleontological Note)	3	595
57.	KRINSLEY, D., Magnesium, strontium, and aragonite in the shells of certain littoral gastropods	4	744
58.	KUMMEL, BERNHARD, Triassic ammonoids from Thailand	4	682
	LANGENHEIM, R. L., JR., see STENSAAS, L. J. (108)		
59.	LAUGHBAUM, L. RONALD, A Paleoecologic study of the upper Denton formation, Tarrant, Denton, and Cooke counties, Texas	6	1183
60.	LEUTZE, W. P., Silurian eurypterids from West Virginia	5	1023
61.	LOCHMAN, CHRISTINA and HU, CHUNG-HUNG, Upper Cambrian faunas from the northwest Wind River Mountains, Wyoming. Part I	5	793
62.	LUNDELIUS, ERNEST, JR. and WARNE, S. ST. J., Mosasaur remains from the Upper Cretaceous of western Australia (Paleontological Note)	6	1215
63.	MACDONALD, J. R., An early Pliocene fauna from Mission, South Dakota	5	961
	MANDWAL, N. K., see BHATIA, S. B. (10)		
	MARTIN, HAROLD, see GREEN, MORTON (37)		
64.	MAWBY, J. E., A new American occurrence of *Heterosorex* Gaillard	5	950
65.	MCGUGAN, A., A new species of the pelecypod *Megalodon* from the Permo-Carboniferous of the Banff area, Alberta	1	101
	MILLER, T. H., see JEFFORDS, R. M. (45)		

66. MUESEBECK, C. F. W., A fossil braconid wasp of the genus *Ecphylus* (Hymenoptera) 3 495
67. MURPHY, M. A. and RODDA, P. U., Mollusca of the Cretaceous Bald Hills formation of California 5 835
68. MURRAY, GROVER E., BOYD, DONALD R,. WOLLEBEN, JAMES A. and WILSON, JOHN A., Late Cretaceous fossil locality, eastern Parras Basin, Coahuila, Mexico (Paleontological Note) 2 368
69. MURRAY, G. E., FURNISH, W. M. and CARILLO B. JOSÉ, Carboniferous goniatites from Caballeros Canyon, State of Tamaulipas, Mexico 4 731
70. NELSON, SAMUEL J., Mississippian lithostrotionid zones of the southern Canadian Rocky Mountains 1 107
71. OLIVER, WILLIAM A., JR., Rugose corals from reef limestones in the Lower Devonian of New York 1 59
72. OLSEN, STANLEY J., Age and faunal relationship of *Tapiravus* remains from Florida 1 164
73. OLSON, EVERETT C., A trilophosaurid reptile from the Kootenai formation (Lower Cretaceous) 3 551
74. OLSSON, RICHARD K., Foraminifera of latest Cretaceous and earliest Tertiary age in the New Jersey Coastal Plain 1 1
75. OSGOOD, R. G., JR. and FISCHER, A. G., Structure and preservation of *Mastopora pyriformis*, an Ordivician dasycladacean alga 5 896
76. PACKARD, E. L., Hypotypes of *Phylloceras onoense* Stanton 3 421
77. PALMER, ALLISON R., Miocene copepods from the Mojave Desert. California 3 447
78. PERRY, T. G. and HATTIN, D. E., Osgood (Niagaran) bryozoans from the type area 4 695
79. PERRY, T. G., and RODRIGUEZ, JOAQUIN, Lectotype of *Anisotrypa symmetrica* Ulrich 2 277
80. PESTANA, H. R., Fossils from the Johnson Spring formation, Middle Ordovician, Independence Quadrangle, California 5 862
81. POPE, J. K., *Sokolophocoleus*, new name for the Machaeridian genus, *Lophocoleus* Ruedemann (Nomenclatural Note) 5 1054
82. PRAKASH, U., A survey of the Deccan Intertrappean flora of India 5 1027
83. PULSE, RICHARD R. and SWEET, WALTER C., The American Upper Ordovician standard. III. Conodonts from the Fairview and McMillan formations of Ohio, Kentucky, and Indiana 2 237
84. RAUP, D. M., Ontogenetic variation in the crystallography of echinoid calcite 5 1041
85. RAW, FRANK, Outline of a theory of origin of the vertebrate 3 497
86. REXROAD, CARL B. and CLARKE, CHARLES R., Conodonts from the Glen Dean formation of Kentucky and equivalent formations of Virginia and West Virginia 6 1202
87. RICH, MARK, *Chaetetes* in the Bird Spring Formation near Lee Canyon, Clark County, Nevada (Paleontological Note) 4 761

RODDA, P. U., see MURPHY, M. A. (67)

RODRIGUEZ, JOAQUIN, see PERRY, T. G. (79)

88. ROHRER, W. L. and KONIZESKI, R., On the occurrence of *Edmontosaurus* in the Hell Creek formation of Montana 3 464
89. ROSS, C. A., Population study of charophyte species, Morrison Formation Colorado 4 717
90. ROSS, JUNE R. P. PHILLIPS, Type species of *Ptilodictya—Ptilodictya lanceolata* (Goldfuss) 3 440
91. ROSS, JUNE PHILLIPS, Re-evaluation of the type species of *Arthropora* Ulrich 5 859
92. ROSS, JUNE PHILLIPS, Larger cryptostome Bryozoa of the Ordovician and Silurian, Anticosti Island, Canada—Part 1 6 1057
93. RUSSELL, D. A., A review of the Oligocene insectivore *Micropternodus borealis* 5 940
94. RUZHENCEV, V. E., Ammonoid classification problems 4 609
95. SABOL, J. W., An emendation of the description of *Nodosaria catesbyi*, d'Orbigny (Paleontological Note) 3 594
96. SADLICK, WALTER, New name for *Spirifer occidentalis* (Girty) and its geologic history 6 1210
97. SCHLAUDT, C. M. and YOUNG, KEITH, Acrothoracic barnacles from the Texas Permian and Cretaceous 5 903
98. SCHMALTZ, L. J., Occurrence of vertebrate remains in Nebraskan till of north-central Missouri (Paleontological Note) 4 762
99. SEILACHER, ADOLF, Epizoans as a key to ammonoid ecology 1 189
100. SELLERS, D. H. A. and FURNISH, W. M., Mississippian ammonoids from Northwestern Canada 6 1124
101. SHAVER, R. H., The Pennsylvanian ostracode *Bairdia oklahomaensis* in Indiana 4 656
102. SILLMAN, LEONARD R., The origin of the vertebrates 3 540
103. SINCLAIR, G. WINSTON, Use of the term "variety" in paleontology (Nomenclatural Note) 1 201
104. SLAUGHTER, BOB H., A new species of *Smilodon* from a late Pleistocene alluvial terrace deposit of the Trinity River 3 486
105. SNYDER, THOMAS E., Fossil termites from Tertiary amber of Chiapas, Mexico (Isoptera) 3 493
106. SOHN, I. G. and BERDAN, JEAN M., The Ostracode family Berounellidae, new 3 479

107. SQUIRES, D. F., *Wellsotrochus*, a new name for *Wellsia* Squires, 1958 (Nomenclatural Note) 5 1053
108. STENSAAS, L. J. and LANGENHEIM, R. L., JR., Rugose corals from the lower Mississippian Joana limestone of Nevada 1 179
109. STEVENS, C. H., JONES, D. H. and TODD, R. G., Ultrasonic vibrations as a cleaning agent for fossils 4 727
110. STUMM, ERWIN C., New rugose corals from the Middle and Upper Devonian of New York 1 161
111. STUMM, ERWIN C., The holotype of *Favosites biloculi* Hall (Paleontological Note) .. 3 589
SWEET, WALTER C., see PULSE, RICHARD R. (83)
112. TASCH, PAUL, Conchostracan genus *Anomalonema* in the American Pennsylvanian. 2 285
113. TEICHERT, CURT, Lehrbuch der Paläozoologie, by A. H. Müller (Review) 2 374
114. TILLMAN, C. G., *Spathacalymene*, an unusual new Silurian trilobite genus 5 891
TODD, R. G., see STEVENS, C. H. (109)
115. TRUJILLO, ERNEST F., Upper Cretaceous Foraminifera from near Redding, Shasta County, California 2 290
116. WALLER, HARRY O., Foraminiferal biofacies off the south China Coast 6 1164
WARNE, S. ST. J., see LUNDELIUS, ERNEST (62)
117. WELLER, J. M., Authorship of name *Mesolobus striatus* (Paleontological Note) 4 762
118. WELLER, J. M., Development of Paleontology 5 1001
119. WHITTINGTON, H. B., *Cordania* and other trilobites from the Lower and Middle Devonian 3 405
120. WILLIAMS, E. G., Marine and fresh water fossiliferous beds in the Pottsville and Allegheny groups of western Pennsylvania 5 908
121. WILSON, J. A., Miocene carnivores, Texas coastal plain 5 983
WILSON, JOHN A., see MURRAY, GROVER E. (68)
122. WINKLER, E. M., Post-Pleistocene ostracodes of Lake Nipissing age 5 923
WOLLEBEN, JAMES A., see MURRAY, GROVER E. (68)
WOOD, A. E., see BURT, A. M. (15)
YOCHELSON, E. L., see CONNORS, J. L. (19)
123. YOUNG, KEITH, Biostratigraphy and the new paleontology 2 347
YOUNG, KEITH, see SCHLAUDT, C. M. (97)

SUBJECT INDEX

Aceton sullivanae: new species, gastropod (67)
Actinocythereis levinsoni: new species, ostracod (10)
Aknisophyllum consuitum: new genus and new species, coral (71)
Alabama: Paleocene coral (43); Pennsylvanian spores (22)
Alabamina jimrothi: new species, foraminifer (115)
Alaska: Paleozoic and Triassic foraminifers and conodonts (8)
Alberta: Permo-Carboniferous pelecypod (65)
Americare: new genus, trilobite (61)
Ammonites: Cretaceous, California (76)
Ammonoids: Cretaceous, Texas (18); Mississippian, Canada (100); Triassic, Thailand (58); classification (94); epizoans, ecology (90); generic names, 1758–1954 (42)
Ampullina mona: new species, gastropod (67)
Ampullina stantoni: new species, gastropod (67)
Anisotrypa symmetrica: Mississippian bryozoan (79)
Anomalina popenoei: new species, foraminifer (115)
Anomalinoides highlandicus: new species, foraminifer (74)
Anomalinoides pseudowelleri: new species, foraminifer (74)
Anomalonema (Anomalonema): new subgenus, conchostracan (112)
Anomalonema (Pierrepruvostia): new subgenus, conchostracan (112)
Anostylostioma vacuolatum: new species, stromatoporoid (31)
Anthaspidella inyoensis: new species, coral (80)
Anticosti: Ordovician and Silurian bryozoans (92)
Aphelognathus irregularis: new species, conodont (83)
Arthropora shafferi: Ordovician bryozoan (91)
Astacolus polandensis: new name, foraminifer (115)
Astrapis: Ordovician, Colorado (29)
Australia: Cretaceous mosasaurs (62)
Axinolobus modulus: new genus and new species, cephalopod (33)
Bairdia oklahomaensis: Pennsylvanian ostracod (101)
Balanus: Hungarian localities (54)
Baltagnostus wyomingensis: new species, trilobite (61)

Barnacles: Permian and Cretaceous, Texas (97)
Beecherella: Paleozoic ostracod (6)
Beecherellidae: Paleozoic ostracods (6)
Belodina leithi: new species, conodont (26)
Berounellidae: new family, ostracods (106)
Biostratigraphy (123)
Bison latifrons: Pleistocene, South Dakota (37)
Blastoid: Mississippian, Missouri (27)
Bolivinoides compressa: new species, foraminifer (74)
Brachiopods: Cambrian, Wyoming (61); Devonian, Canada (21), Nova Scotia (12); Pennsylvanian, Missouri (39); Permian, Queensland (16); *Spirifer occidentalis* (Girty) (96)
Brachyelasma bassleri: new species, coral (80)
Branchiopods: Devonian, Germany (50)
Briantelasma americanum: new genus and new species, coral (71)
Briantelasma knoxboroense: new genus and new species, coral (71)
Bryozoans: Ordovician, Anticosti (92), *Arthropora* (91); Silurian, Anticosti (92), England, Germany, Gotland (90), Indiana (78); Mississippian, Kentucky (79), Utah (14)
Bulmina hornerstowensis: new species, foraminifer (74)
Bulimina pseudocacumenata: new species, foraminifer (74)
Calcisphaera: Mississippian, Illinois (5)
California: Cretaceous ammonites (76), Foraminifera (115), mollusks (67), pelecypods (49); Miocene copepods (77); Ordovician corals (80); Permian corals (24); Pliocene gastropods (32); Recent foraminifera (3)
Cambrian: faunas, Wyoming (61); loricates, North America (7)
Canada: Devonian brachiopods (21), stromatoporoids (31); Mississippian ammonoids (100), corals (70)
Candona poseyensis: new species, ostracod (122)
Caninia trojana: new species, coral (24)
Carboniferous: cephalopods, U. S. A. (33); *Chaetetes,* Nevada (87); goniatites, Mexico (69)
Cephalopods: Carboniferous, North America (33); Cretaceous, California (67), Oregon (48)
Ceramopera vesicularis: new species, bryozoan (78)
Chaetetes: Carboniferous, Nevada (87)
Chelodes depressus: new species, loricate (7)
Chelodes intermedius: new species, loricate (7)
Chimaerotheca gilli: new name, egg case (25)
China: Recent foraminiferal biofacies (116)
Cibicides compressa: new species, foraminifer (74)
Cleoniceras? dilleri: new species, cephalopod (48)
Clinura anassa: new species, gastropod (67)
Coelogasteroceras coxi: new name, cephalopod (33)
Colorado: Jurassic charophytes (89); Oligocene rodents and lagomorphs (15); Ordovician neurodontiformes and *Astrapis* (29)
Composita tetralobata: new species, brachiopod (39)
Conchostracan: Pennsylvanian, Pennsylvania (112)
Conodonts: Ordovician, Manitoba (26), Ohio, Kentucky, Indiana (83); Mississippian, Kentucky, Virginia, West Virginia (86); Paleozoic and Triassic, Alaska (8); magnetic separation (23)
Copepods: Miocene, California (77)
Corals: Ordovician, California (80); Devonian, New York (71, 110, 111); Mississippian, Canada (70), Nevada (108); Permian, Nevada and California (24); Paleocene, Alabama (43); classification (55)
Cordania: Devonian trilobite (119)
Cordania falcata: new species, trilobite (119)
Cretaceous: alga, Guatemala (47); ammonoids, California (76), Texas (18); barnacles, Texas (97); cephalopods, Oregon (48); Denton formation, Texas (59); dinosaur, Montana (88); Foraminifera, New Jersey (74), California (115); Maestrichtian type locality (41); mollusks, California (67), Mexico (68); mosasaurs, Australia (62); ostracods, New Jersey (1); pelecypods, Oregon (48); West Coast, U.S.A. (49); plants, India (82); reptile, Montana (72)
Cribrostomoides californiensis: new species, foraminifer (115)
Crystallography: echinoid calcite (84)
Cylichna andersoni: new species, gastropod (67)
Cynomys spispiza: new species, prairie dog (36)
Cyphotrypa osgoodensis: new species, bryozoan (78)
Cypria nipissingae: new species, ostracod (122)
Cyprus: Triassic hydrozoan (28)
Cyrtoniodus sinclairi: new species, conodont (26)
Dentalina crosswicksensis: new species, foraminifer (74)
Dentalina(?) pseudoaculeata: new species, foraminifer (74)

Dentalina rancocasensis: new species, foraminifer (74)
Dentalina toulmini: new species, foraminifer (74)
Depasophyllum tabulatum: new species, coral (110)
Desmoinesia: new genus, brachiopod (39)
Devonian: brachiopods, Nova Scotia (12), Canada (21); brachiopod, Germany (50); corals, New York (71, 110, 111); stromatoporoids, Canada (31); trilobites, Quebec, Maine, New York, Tennessee, Oklahoma (119)
Diatomaceous earth: Pleistocene, Nebraska (4)
Dictyoclostus tiawahensis: new species, brachiopod (39)
Dielymella? trituberculata: new species, conchostracan (61)
Dorothia monmouthensis: new species, foraminifer (74)
Echinoids: crystallography of calcite (84)
Ecology: epizoans, ammonoids (90)
Ecphylus oculatus: new species, wasp (66)
Edaphocyon pointblankensis: new genus and new species, carnivore (121)
Edmontosaurus: Cretaceous dinosaur (88)
England: Jurassic foraminiferans (17), Silurian bryozoan (90)
Eocene: corkwood, United States (13)
Eofletcheria kearsargensis: new species, coral (80)
Eogunnarites matsumotoi: new species, cephalopod (67)
Eoligonodina fairmountensis: new species, conodont (83)
Eolissochonetes bilobatus: new genus and new species, brachiopod (39)
Epizoans: ammonoid ecology (90)
Eponides bandyi: new species, foraminifer (115)
Eponides birdi: new species, foraminifer (115)
Eponides goudkoffi: new species, foraminifer (115)
Eponides greatvalleyensis: new species, foraminifer (115)
Eucypris tuberculata: new species, ostracod (122)
Eurypterids: Silurian, West Virginia (60)
Euspira marianus: new species, gastropod (67)
Euspira popenoei: new species, gastropod (67)
Favosites biloculi: Devonian coral (111)
Fayettevillea planorbis: new genus and new species, cephalopod (33)
Fenestella acarinata: new species, bryozoan (14)
Fenestella (Minilya) crockfordae: new species, bryozoan (14)
Fenestella dissepinodaria: new species, bryozoan (14)
Fenestella hamilhensis: new species, bryozoan (14)
Fenestella (Minilya) incipiens: new species, bryozoan (14)
Fenestella serratula humbugensis: new subspecies, bryozoan (14)
Fenestella tooelensis: new species, bryozoan (14)
Fenestralia trifurcata: new species, bryozoan (14)
Fenestella utahensis: new species, bryozoan (14)
Ferestromatopora jacquesensis: new species, stromatoporoid (31)
Fistulipora promiscua: new species, bryozoan (78)
Fletcherina incognita: new species, coral (71)
Florida: Tertiary tapir (72)
Fluminicola sanmateoensis: new species, gastropod (32)
Foraminifera: Pennsylvania, Kansas (44); Paleozoic and Triassic, Alaska (8); Jurassic, England (17); Cretaceous, California (115); Cretaceous-Tertiary, New Jersey (74); Miocene, Virginia (95); Recent, California (3), China coast (116); photography (38)
Frondicularia durrelli: new species, foraminifer (115)
Fusulinids: Permian, Guatemala (53)
Gastropods: Cretaceous (67) and Pliocene (32), California; Pleistocene, Nebraska (30); contained minerals (57)
Gaudryina bulloides: new species, foraminifer (74)
Gaudryina monmouthensis: new species, foraminifer (74)
Gavelinella limbata: new species, foraminifer (74)
Germany: Devonian branchiopod (50); Silurian bryozoan (90)
Globigerina pachyderma: Recent foraminifer (3)
Globorotalia crosswicksensis: new foraminifer (74)
Globorotalia monmouthensis: new species, foraminifer (74)
Globorotalia redbankensis: new species, foraminifer (74)
Globotruncana monmouthensis: new species, foraminifer (74)
Glyptoglossella: new name, brachiopod (20)
Goniatites: Carboniferous, Mexico (69)
Gotland: Silurian bryozoan (90)
Graptolites: Silurian, Maine (9)

Grewingkia whitei: new species, coral (80)
Guatemala: Cretaceous alga (47); Permian fusulinids (53)
Gyrodes allisoni: new species, gastropod (67)
Gyrodes greeni: new species, gastropod (67)
Gyroidinoides imitata: new species, foraminifer (74)
Haplophragmoides sewellensis: new species, foraminifer (74)
Hemitrypa reticulata: new species, bryozoan (14)
Henningopora apta: new species, bryozoan (78)
Heterastridium conglobatum conglobatum: Triassic hydrozoan (28)
Heterosorex: Miocene vertebrate (64)
Heterotermes primaevus: new species, termite (105)
Heterotrypa? perplexa: new species, bryozoan (78)
Homevalia pelicanensis: new species, brachiopod (16)
Hungary: *Balanus* localities (54)
Hydrozoan: Triassic, Cyprus (28)
Illinois: Mississippian calcispheres (5)
India: Cretaceous-Eocene Deccan plants (82); Miocene ostracods (10)
Indiana: Ordovician conodonts (83); Pennsylvanian ostracod (101); Silurian bryozoans (78), trilobite (114)
Ingelarella havilensis: new species, brachiopod (16)
Ingelarella ingelarensis: new species, brachiopod (16)
Ingelarella magna: new species, brachiopod (16)
Ingelarella mantuanensis: new species, brachiopod (16)
Ingelarella plana: new species, brachiopod (16)
Ingelarella plica: new species, brachiopod (16)
Insects: Tertiary, Mexico: wasp (66), termites (105)
Johnson Spring formation: Ordovician, California (80)
Josina festiva: new genus and new species, trilobite (61)
Jurassic: charophytes, Colorado (89); Foraminifera, England (17)
Kansas: Pennsylvanian Foraminifera (44)
Kentucky: Mississippian bryozoan (79), conodonts (86); Ordovician conodonts (83)
Lagena distincta: new species, foraminifer (74)
Lagena pseudocostata: new species, foraminifer (74)
Lagena rancocasensis: new species, foraminifer (74)
Lagenidae: Jurassic Foraminifera (17)
Lamarckina praenaheolensis: new species, foraminifer (74)
Lamarckina reedana: new species, foraminifer (115)
Leitneria eocenica: new combination, corkwood (13)
Lenticulina californiensis: new species, foraminifer (115)
Lichenaria sisyphi: new species, coral (80)
Lingulina californiensis: new species, foraminifer (115)
Lingulina lucillea: new species, foraminifer (115)
Linoproductus distortus: new species, brachiopod (39)
Linoproductus echinatus: new species, brachiopod (39)
Linoproductus planiventralis: new species, brachiopod (39)
Lithostrotion connorsensis: new species, coral (24)
Lithostrotion dilatata: new species, coral (24)
Lithostrotion mokomokensis: new species, coral (24)
Lithostrotion princeps: new species, coral (24)
Lithostrotion warreni: new species, coral (70)
Lithostrotionella bailliei: new species, coral (70)
Lithostrotionella stelcki: new species, coral (70)
Lonsdaleia cordillerensis: new species, coral (24)
Lonsdaleia illipahensis: new species, coral (24)
Loricates: Cambian and Ordovician, North America (7)
Macgeea ponderosa: new species, coral (110)
Maestrichtian: type locality (41)
Maine: Devonian trilobites (119); Silurian graptolites (9)
Manitoba: Ordovician conodonts (26)
Marginulina loisana: new species, foraminifer (115)
Marginulinopsis praetschoppi: new species, foraminifer (115)
Mariella (Mariella) fricki: new species, cephalopod (67)
Marssonella conica: new species, foraminifer (74)
Mastopora pyriformis: Ordovician alga (75)
Megalodon banffensis: new species, pelecypod (65)
Mesolobus striatus: new species, brachiopod (39)
Mesolobus striatus: authorship (117)

Mexico: Carboniferous goniatites (69); Cretaceous mollusks and dinosaurs of Hipolito (68); Oligocene or Miocene wasp (66); Tertiary termites (105)
Michigan: Recent ostracods (122)
Micropternodus borealis: Oligocene insectivore (93)
Mictophyllum orientalis: new species, coral (110)
Minicephalus primus: new genus and new species, trilobite (61)
Miocene: algae, Oregon (35); carnivores, Texas (121); copepods, California (77); Foraminifera, Virginia (95); *Heterosorex*, Oregon (64); ostracods, India (10)
Mississippi: Pennsylvanian spores (22)
Mississippian: ammonoids, Canada (100); blastoid, Missouri (27); bryozoans, Utah (14), Kentucky (79); calcispheres, Illinois (5); conodonts, Kentucky, Virginia, West Virginia (86); corals, Canada (70), Nevada (108)
Missouri: Mississippian blastoid (27); Pennsylvanian brachiopod (39); Pleistocene vertebrates (98)
Mitorthoceras perfilosum: new genus and new species, cephalopod (33)
Mollusks: Cretaceous, Mexico (68)
Monograptus forbesi: new species, graptolite (9)
Monograptus tumescens contus: new variety, graptolite (9)
Monograptus vulgaris ashlandensis: new variety, graptolite (9)
Monotrypa exserta: new species, bryozoan (78)
Montecaris lehmanni: new species, branchiopod (50)
Montian: type locality (41)
Montana: Cretaceous dinosaur (88), reptile (73); Oligocene insectivore (93)
Mystrocephala: new genus trilobite (119)
Nebraska: Pleistocene diatomaceous earth (4), gastropod (30)
Neoglyphioceras hyatti: new name, cephalopod (33)
Neospirifer goreii brevimarginatus: new variety, brachiopod (39)
Neurodontiformes: Ordovician, Colorado (29)
Nevada: Carboniferous *Chaetetes* (87); Mississippian corals (108), Permian (24)
New Jersey: Cretaceous-Tertiary, foraminifera (74), ostracods (1)
New York: Devonian corals (71, 110, 111), trilobites (119)
Nodosarella irregularis: new species, foraminifer (74)
Nodosarella monmouthensis: new species, foraminifer (74)
Nodosarella wintereri: new species, foraminifer (115)
Nodosaria catesbyi, emend.: Miocene foraminifer (95)
Nodosaria redbankensis: new species, foraminifer (74)
Nodosaria spinosa: new species, foraminifer (74)
Nodosaria spinosa: new species, foraminifer (74)
North America: Cambrian loricates (7); Mississippian cephalopods (33); Ordovician loricates (7)
Notospirifer minutus: new species, brachiopod (16)
Nova Scotia: Devonian brachiopods (12)
Ohio: Ordovician conodonts (83)
Oklahoma: Devonian trilobites (119)
Oligocene: insectivore, Montana (93); rodents and lagomorphs, South Dakota and Colorado (15)
Ordovician: alga, Virginia (75); bryozoans, Anticosti (92), *Arthopora* (91); conodonts, Manitoba (26), Ohio, Kentucky, Indiana, (83); corals, California (80); loricates, North America (7); neurodontiformes and *Astraspis*, Colorado (29)
Oregon: Cretaceous cephalopods (48), pelecypods (48, 49); Miocene algae (35), *Heterosorex* (64)
Ostracods: Pennsylvanian, Indiana (101); Cretaceous and Tertiary, New Jersey (1); Miocene, India (10); Recent, Michigan (122); A. M. Norman species (11); *Beecherella* and Beecherellidae (6); Berounellidae, n. fam. (106)
Oulodus casteri: new species, conodont (83)
Pachyglossella: new name, brachiopod (20)
Paleocene: coral, Alabama (43); Montian type locality (41).
Paleoecology: Cretaceous Denton formation, Texas (59)
Paleontology: history (118)
Paleophyllum mazourkensis: new species, coral (80)
Paleopsephaea sacramentica: new species, gastropod (67)
Paleozoic: Foraminifera and conodonts, Alaska (8)
Paracravenoceras ozarkense: new genus and new species, cephalopod (33)
Parafusulina biturbinata: new species, fusulinid (53)
Parafusulina erratoseptata: new species, fusulinid (53)
Parafusulina subrectangularis: new species, fusulinid (53)
Parapholyx durhami: new species, gastropod (32)
Parapuzosia: Cretaceous, Texas (18)
Parrella convexa: new species, foraminifer (74)
Pelecypods: Permo-Carboniferous, Alberta (65); Cretaceous, Oregon (48), West Coast (49)

Pennsylvania: Pennsylvania conchostracan (112); Pottsville and Allegheny faunas (120)
Pennsylvanian: brachiopods, Missouri (39); conchostracan, Pennsylvania (112); Foraminifera, Kansas (44); ostracod, Indiana (101); Pottsville and Allegheny faunas, Pennsylvania (120); spores, Mississippi and Alabama (22); Tensleep fauna, Wyoming (40)
Permian: barnacles, Texas (97); brachiopods, Queensland (16); corals, Nevada and California (24); fusulinids, Guatemala (53)
Permo-Carboniferous: pelecypod, Alberta (65)
Pernerina redbankensis: new species, foraminifer (74)
Peripetoceras whitei: new name, cephalopod (33)
Phylloceras onoense: Cretaceous ammonite (76)
Planorbula vulcanata: Pleistocene gastropod (30)
Plants: Cretaceous-Eocene, India (82); algae, Ordovician, Virginia (75), Cretaceous, Guatemala (47), Miocene, Oregon (35); Jurassic charophytes, Colorado (89); Eocene corkwood, U.S.A. (13); Pennsylvanian spores, Alabama and Mississippi (22)
Planularia howelli: new species, foraminifer (74)
Pleistocene: bison, South Dakota (37); diatomaceous earth, Nebraska (4); gastropod, Nebraska (30); sabertooth cat, Texas (104); vertebrates, Texas (46), Missouri (98)
Pleurostomella greatvalleyensis: new species, foraminifer (115)
Pliocene: gastropods, California (32); mammals, South Dakota (63)
Polypora micronodosa: new species, bryozoan (14)
Polypora stansburyensis: new species, bryozoan (14)
Praeglobotruncana hansbolli: new species, foraminifer (115)
Preacanthochiton cooperi: new genus and new species, loricate (7)
Preacanthochiton depressus: new genus and new species, loricate (7)
Preacanthochiton productus: new genus and new species, loricate (7)
Preacanthochitonidae: new family, loricates (7)
Prioniodina velicuspis: new species, conodont (83)
Procamelus foxi: new species, camel (63)
Prolecanites warreni: new species, ammonoid (100)
Pseudobiothrophyllum arrectum: new genus and new species, coral (71)
Pseudoblothrophyllum helderbergium: new genus and new species, coral (71)
Pseudoblothrophyllum munnsvillium: new genus and new species, coral (71)
Pseudoparrella minuta: new species, foraminifer (74)
Pterotrigonia: Cretaceous pelecypod (49)
Ptilodictya denticulata: new species, bryozoan (92)
Ptilodictya lanceolata: Silurian bryozoan (90)
Ptychoblastus pustulosus: new genus and new species, blastoid (27)
Ptychopleurella arthuri: new species, brachiopod (80)
Ptylopora condrai: new species, bryozoan (14)
Ptylopora eliasi: new species, bryozoan (14)
Puzosia puma: new species, cephalopod (67)
Puzosia sullivanae: new species, cephalopod (67)
Pycnoporidium sinusosum: new species, alga (47)
Pygmaeoceras: new genus, cephalopod (33)
Quebec: Devonian trilobites (119)
Queensland: Permian brachiopods (16)
Rayonnoceras foerstei: new name, cephalopod (33)
Recent: Foraminifera, California (3), China coast (116); ostracods, Michigan (122)
Reinholdella brotzeni: new species, foraminifer (74)
Reticycloceras croneisi: new genus and new species, cephalopod (33)
Reviews: (2, 19, 34, 51, 52, 113)
Robulus hornerstownensis: new species, foraminifer (74)
Robulus jenningsi: new species, foraminifer (74)
Robulus rancocasensis: new species, foraminifer (74)
Rogerella cragini: new species, barnacle (97)
Rugoglobigerina jerseyensis: new species, foraminifer (74)
Rugoglobigerina kingi: new species, foraminifer (115)
Rugoglobigerina praehelvetica: new species, foraminifer (115)
Saracenaria cowcreekensis: new species, foraminifer (115)
Seabrookia stewarti: new species, foraminifer (74)
Septopora ulrichi: new species, bryozoan (14)
Silurian: bryozoans, Anticosti (92), Indiana (78), England, Germany, Gotland (90); eurypterids, West Virginia (60); graptolites, Maine (9); trilobite, Indiana (114)
Siphonophrentis variabilis: new species, coral (71)
Smilodon trinitiensis, new species, sabertooth cat (104)
Sokolophocoleus: new name, echinoderm (81)

Sollariella stewarti: new species, gastropod (67)
South Dakota: Oligocene rodents and lagomorphs (15); Pleistocene bison (37); Pliocene mammals (63); Tertiary prairie dog (36)
Spathacalymene: new genus, trilobite (114)
Spirifer occiduus: new name, brachiopod (96)
Stigmatella dubia: new species, bryozoan (78)
Streptelasma tennysoni: new species, coral (80)
Stringocephalus chasmognathus: new species, brachiopod (21)
Stringocephalus glaphyrus: new species, brachiopod (21)
Stringocephalus sapiens: new species, brachiopod (21)
Stromatopora arcuata: new species, stromatoporoid (31)
Stromatoporoids: Devonian, Canada (31)
Stropheodonta (Rhenostrophia): new subgenus, brachiopod (12)
Taleastroma lenzi: new species, stromatoporoid (31)
Taleastroma vitreum: new species, stromatoporoid (31)
Tapiravus polkensis: new species, tapir (72)
Techniques: magnetic separation of conodonts (23); measuring internal volumes of shells (56); photography (38, 45); ultrasonic cleaning (109)
Tennessee: Devonian trilobites (119)
Tensleep fauna: Pennsylvanian, Wyoming (40)
Tertiary: Foraminifera, New Jersey (74); ostracods, New Jersey (1); plants, India (82); prairie dog, South Dakota (36); tapir, Florida (72); termites, Mexico (105); wasp, Mexico (66)
Tessarolax trinalis: new species, gastropod (67)
Texas: Cretaceous ammonoid (18), barnacles (97), Denton formation (59); Miocene carnivores (121); Permian barnacles (97); Pleistocene sabertooth cat (104), vertebrates (46)
Thailand: Triassic ammonoids (58)
Thamniscus raribifurcatus: new species, bryozoan (14)
Toxolophosaurus cloudi: new genus and new species, reptile (73)
Triassic: ammonoids, Thailand (58); conodonts and Foraminifera, Alaska (8); hydrozoan, Cyprus (28)
Trilobites: Cambrian, Wyoming (61); Silurian, Indiana (114); Devonian, Quebec, Maine, New York, Tennessee, Oklahoma (119)
Trochammina sewellensis: new species, foraminifer (74)
Tryplasma fascicularium: new species, coral (71)
Turbinolia rosetta: new species, coral (43)
Turrilites (Turrilites) dilleri: new species, cephalopod (67)
Utah: Mississippian bryozoans (14)
Vaginulina crosswicksensis: new species, foraminifer (74)
Vaginulina marginata: new species, foraminifer (74)
Vaginulinopsis reddingensis: new species, foraminifer (115)
Valvulineria marianosi: new species, foraminifer (115)
Variety, use of: (103)
Verneuilina monmouthensis: new species, foraminifer (74)
Vertebrates: Pleistocene, Missouri (98), Texas (46); origin (85, 102); Pleistocene bison, South Dakota (37); Miocene carnivore, Texas (121); Cretaceous dinosaurs, Mexico (68), Montana (88); Miocene *Heterosorex*, Oregon (64); Oligocene insectivore, Montana (93); Oligocene lagomorphs, South Dakota and Colorado (15); Pliocene mammals, South Dakota (63); Cretaceous mosasaurs, Australia (62); Tertiary prairie dog, South Dakota (36); Cretaceous reptile, Montana (73); Oligocene rodents, South Dakota and Colorado (15); Pleistocene sabertooth cat, Texas (104); Tertiary tapir, Florida (72)
Virginia: Miocene foraminifer (95); Mississippian conodonts (86); Ordovician alga (75)
Wellsotrochus: new name, coral (107)
West Virginia: Mississippian conodonts (86); Silurian eurypterids (60)
Woodringina hornerstownensis: new species, foraminifer (74)
Wyoming: Cambrian faunas (61); Pennsylvanian Tensleep fauna (40)
Zygognathus maysvillensis: new species, conodont (83)

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